

## Ecological Evaluation of Potential Overabundance of Ungulates in U.S. National Parks: A Case Study

By

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**Abstract.** We conducted a study into the possibility of overabundance or overconcentration of elk (*Cervus elaphus*) and human alterations of elk habitat in Rocky Mountain National Park and the adjacent town of Estes Park, Colorado. National Park Service (NPS) policy is clear that an overabundance and unnatural concentration of ungulates can be managed, but ambiguities and vagueness exist in the ecological literature as to what constitutes an overabundance of ungulates. We reviewed the utility of applying five different ecological views or approaches--the ungulate population-predator limitation, biodiversity, sustainability/grazing optimization, overgrazing, and allowable use approaches--to a case study of a potential overabundance of elk. Unfortunately, most of the approaches available to ecologists were developed with goals in mind that were very different from goals for a national park. For example, the sustainability, overgrazing, and allowable use approaches were all originally developed with maximum secondary production by ungulates as the primary goal in mind. Our goal was to search these common views and methods for those approaches that were the most clear, easiest to apply, unambiguous, and most closely allied to National Park Service policy and guidelines. Elk within Rocky Mountain National Park increased to levels approximating food-limited carrying capacity ( $K$ ) following release from human controls (live capture and removals) within the park in 1968. Estimates of the food-limited  $K$  using forage/nutritional-based methodology in the park averaged  $1,154 \pm 163$  elk ( $\bar{x} \pm se$ ), while independent density-dependent population-based estimates of  $K$  were similar at  $1,069 \pm 55$ . Elk populations in the park stabilized approximately at these numbers over the previous 10 years (2001 population estimate =  $1,074 \pm 39$  elk). However, elk numbers in the town sector averaged  $1,975 \pm 150$  in 2001, and elk in town were still increasing. Our estimates of food-limited  $K$  that elk could eventually grow to in the town sector were  $2,869 \pm 415$  elk, based on population analyses and ranged from  $3,082 \pm 103$  to  $3,391 \pm 113$  elk, based on forage estimates for an average year (based on 50–55% consumption rate). In a dry year, the forage-based estimate of the potential for elk the area could support was lower, ranging from  $2,330 \pm 78$  to  $2,563 \pm 85$  elk. The forage base for elk in town was artificially enhanced in a few locales due to fertilization and irrigation of human-altered grassland types such as pastures, lawns, and golf courses. The habituation of elk toward humans in the town sector allow them to use these rich forages and other grassland habitats in an area that is lower in elevation, has less snow cover, and also likely has fewer predators due to the human developments than does the park sector. However, these human increases to the elk forage base in town were more than balanced by losses to human activities such as housing developments and water impoundments on former usable riparian winter range. We estimated the town could support about 169 fewer elk following the human modifications than before the human developments took

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place. Elk negatively influenced seven different willow growth parameters in the park ( $P < 0.001$ ) when elk numbers reached approximate densities of  $32 \pm 1$  elk/km<sup>2</sup> and when consumption exceeded about 37%. Consumption rates of willow by elk averaged  $30 \pm 2\%$  of the current annual shrub growth across the winter range, but grazing optimization, i.e., greater peak production of grazed willows compared to ungrazed willows, occurred at levels lower than this where moderate consumption rates of about 21% occurred on willows. On grazed grassland sites, there was a minor increase in bare ground. Also, the cover or production of three forb species decreased when compared to similar paired nearby plots that were ungrazed for 4 years. Herbaceous biomass production was 22% less ( $P < 0.05$ ) in grazed willow sites compared to these paired ungrazed sites. There was no grazing treatment effect on plant species diversity in upland grass/shrub or willow. There also was no overall decline in nitrogen (N) and few changes in other macronutrient concentrations in plant tissues and few effects on root biomass or root N attributed to ungulate herbivory, except some increases in coarse root biomass occurred on grazed herbaceous communities. But in willow communities grazed for 35 years in the park, a decline in fine root biomass, root N concentrations, and aboveground N yield were observed compared to ungrazed sites ( $P < 0.10$ ). We also found 79% lower N mineralization ( $P = 0.07$ ) and 78% lower  $\text{NO}_3^-$  pools ( $P = 0.01$ ) in grazed short willows compared to willows that were ungrazed for 4 years.

We concluded that the ungulate population-predator limitation and forage-based estimates of food-limited  $K$  approaches, and the overgrazing approach, were the most specific and readily measurable approaches to apply to the question of a possible overabundance of elk. However, population-based limitation estimates required many years of data and considerable cost and effort. National Park Service policy calls for preservation of natural processes, and predation effects were a major natural process potentially limiting ungulates. Restoration of all large capable predators, or in cases such as in RMNP where that may no longer be feasible, management intervention to duplicate this predator limitation, appears to be the approach that is closely aligned to NPS policy and guidelines. Recent information following the wolf (*Canis lupus*) restoration into Yellowstone National Park (YNP) suggests that the same multiple predators in RMNP (grizzly bears [*Ursus arctos*], coyotes [*Canis latrans*], in concert with wolves) might limit elk populations moderately (15–30%) below food-limited  $K$ . The overgrazing approach is simple to apply and this simple approach is the fastest to apply to clear-cut cases of severe overgrazing, or of no overgrazing. However, for those more ambiguous cases of intermediate effects that are more often the case, the approach can be oversimplistic for complex ecological systems. We concluded the allowable use approach could be readily applied to a park ecosystem, but only if park staff conducted considerable sampling of the effects on plants of different ungulate use levels. Our review of the published literature indicated no generalized guidelines for appropriate use levels, but instead plant responses to a specific level of consumption varied considerably by the evolutionary history of grazing in the area, climate, pre-adaptations of the plants to grazing (e.g., plants with prostrate growth and larger belowground root reserves are less sensitive to grazing), and season of the herbivore use. We concluded that application of the biodiversity and sustainability approaches were not as readily applicable to park managers, since those views were dependent on knowledge of complex ecosystem responses to ungulates and judgments as to the level of ungulate effects and plant changes considered acceptable in light of NPS mandates and policies. However, these approaches were also closely aligned to NPS policy and guidelines. Thus, their application is encouraged in those park ecosystems with extensive knowledge of ecological processes and conditions, such as is the case for RMNP. All of the approaches could potentially be useful to apply to a national park situation, providing there is adequate ecological information available.

**Keywords:** Allowable use, *Cervus elaphus*, elk, grazing, national park management, natural regulation, sustainability, ungulates.

## Introduction

National Park Service (NPS) policy states that natural processes should be permitted to maintain wildlife populations in national parks to the largest extent possible (National Park Service 2001). Human activities have greatly altered some national park ecosystems from their pre-existing, natural state. Native predators have been eliminated in many national parks, migrations of ungulates have been altered by developments and activities outside of parks, keystone predator species may have been lost or their populations altered, and climate change may have altered ecosystems (Wagner et al. 1995a; Wright 1996; Singer et al. 1998a).

Many national parks manage ungulates according to natural regulation, or "hands-off", management within the parks. While natural regulation is largely consistent with the enabling legislation for U.S. national parks (NPS Organic Act of 1916; Leopold et al. 1963; Keiter 1988), the policy has been criticized for being based on inadequately tested scientific hypotheses (Wagner et al. 1995a). The natural regulation policy has been alternatively supported (Houston 1971, 1982; Yellowstone National Park 1997) and criticized (Kay and Wagner 1994; Wagner et al. 1995a) in the ecological literature. The criticisms of natural regulation point out the lack of limitation of ungulates due to extirpation of large wild mammalian predators in many parks (Lime et al. 1993; Peterson 1999), the absence of Aboriginal human control of ungulates (Kay 1994), and major alterations of ungulate migrations (Skinner 1928; Pengelly 1963; Chase 1986). Natural regulation management may also be operationally vague. The policy has been applied alternatively to park ecosystems with extirpated large predators and altered migrations (Cole 1971; Houston 1971, 1982), or to systems with migrations and large predators intact (Wright 1996; Yellowstone National Park 1997). NPS policy clearly states that unnaturally high populations of wildlife that are due to modern human activities may be controlled (NPS 2001). But the definition of an overconcentration or overabundance of ungulates may be vague and ambiguous in the ecological literature (Caughley 1976; McNab 1985; Keiter 1988; Wagner et al. 1995a; McShea et al. 1997; Boyce 1998).

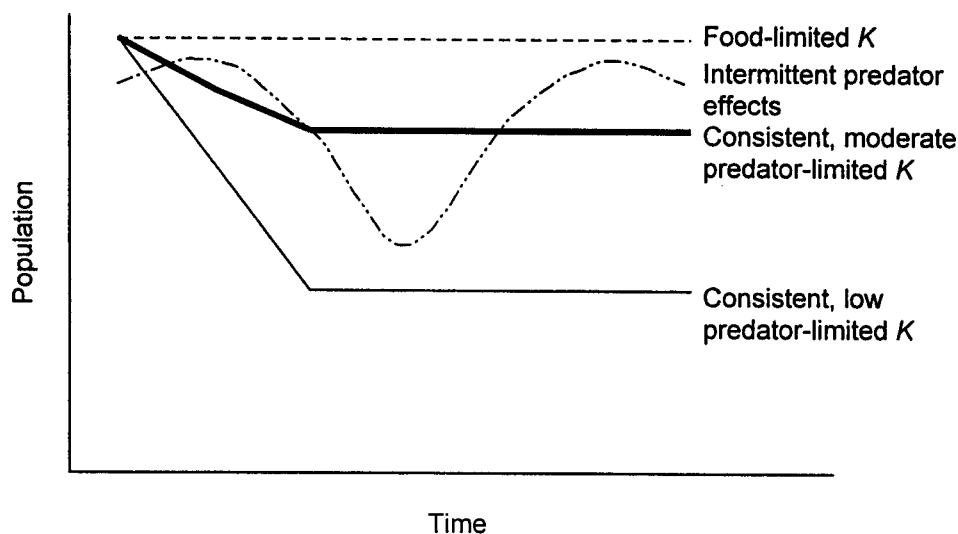
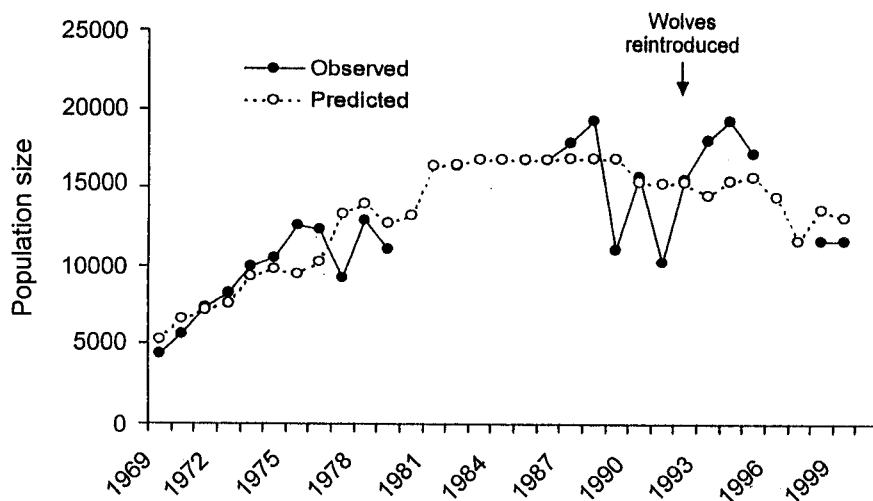
Several commonly used approaches and their criteria exist in the ecological literature that may help guide managers during the evaluation of the appropriate numbers of ungulates in national parks. Our purpose was to review these approaches and apply them to a case study of the potential overabundance of elk (*Cervus elaphus*)

in Rocky Mountain National Park (hereafter RMNP) and the adjacent town of Estes Park, Colorado. Our goal was to select an approach where both the key measures, and the logic of the paradigm or approach, were unambiguous, easy to apply, and closely aligned to NPS policy and guidelines.

### *Ungulate Population-Predator Limitation Approach*

The analysis of ungulate populations could be the central focus of a park manager's assessment of ungulate abundance. For example, the estimation of food-limited ecological carrying capacity (hereafter food-limited  $K$ ) is central to all population-based analyses. Food-limited  $K$  can be determined from: (a) linear and nonlinear density feedback relationships (Caughley 1976; Houston 1982; Boyce 1989); or (b) nutritional, GIS-assisted forage-based methods (Hobbs et al. 1982; Coughenour and Singer 1996). Populations at food-limited  $K$  are assumed to be regulated within some range by density-dependent processes caused by animal per capita restrictions in food availability (Caughley 1976; Dublin et al. 1990). The process of forage restriction in ungulates near food-limited  $K$  may also result in reductions in plant cover and production, plant species alterations, reduced body condition of ungulates, reduced survival rate of ungulates, and subsequently, a new and lower equilibrium between ungulates and forage conditions (Caughley 1976; Sinclair et al. 1985).

Predator limitation of ungulates below food-limited  $K$  may occur under natural conditions. Predators may limit ungulates either slightly below (7%–30%) food-limited  $K$  (Boutin 1992; Boyce 1993; Mack and Singer 1993), well below (40%–60%) food-limited  $K$  (Gasaway et al. 1992; Lime et al. 1993; Messier 1994), or the limitation may be highly variable over time (Fig. 1a). For example, a highly variable, predator-sensitive scenario was identified where predators remove vulnerable individuals and may periodically limit ungulates only during severe weather when there are more vulnerable individuals (McLaren and Peterson 1994; Sinclair and Arcese 1995; Mech et al. 1998). Limitation is more likely where there are multiple predators. Orians et al. (1997) and Peterson (1999) concluded that where both wolves and bears (*U. arctos*, *U. americanus*) coexist, ungulates are limited to lower densities than in cases where only bears or wolves occur. Additionally, a fourth alternative potential form of limitation, the Aboriginal overkill hypothesis of Kay

**a****b**

**Fig. 1.** Schematic representation of  $K$ , the ecological or food-limited carrying capacity for an ungulate released from human controls, such as elk were in both Rocky Mountain and Yellowstone National Parks. Also represented are several examples from the literature of moderate (Lime et al. 1993), large (Gasaway et al. 1983; Messier 1995), and very large (Kay 1994) limitations of ungulates. Most ungulate-vegetation or ungulate-predator limited systems regularly fluctuate 15% or more over short time scale, while longer term, large fluctuations, or shifts between these scenarios are also possible (a). The expected and observed elk population size in Yellowstone National Park before and after wolf reintroduction (Singer et al. 2002) (b).



(1994, 1998) states that Native Americans reduced ungulates, such as elk, by as much as 90–95% or more below food-limited  $K$ , although evidence for this view is limited (Boyce 1998; Yochim 2001). Also, ungulates might not necessarily be overpopulated, but alterations in movements and migrations might cause an overconcentration.

Population-based approaches may be useful in that the population analyses, their evaluation, and the subsequent management responses can be immediate. In addition, there is an ever-growing body of evidence in the scientific literature for suggesting predator-limitation of ungulates occurs in natural systems (Gasaway et al. 1992; Mech et al. 1998; Singer et al. 1998a). The approach also lends itself well to adaptive management, since the management goal is a specific population size, but the vegetation expectations of that goal can be periodically evaluated and modified, if necessary. Unfortunately for managers, a large degree of uncertainty continues to exist over the precise extent of predator limitation of ungulates and the variability of predator limitation in undisturbed, pre-European herbivore-predator systems (Boutin 1992; Singer et al. 1997). Further constraining application to the RMNP case, nearly all the evidence of limitation comes from studies of moose (*Alces alces*) and caribou (*Rangifer tarandus*), and little research has been conducted on potential limitation of elk (Jedrzejewska and Jedrzejewski 1998; Singer et al. 2002).

The most applicable example comes from the recent reintroduction of gray wolves into Yellowstone National Park (YNP). Potential limitation of this elk population by wolves was recently modeled by Singer et al. (2002). The dynamics of this elk population are some of the best understood. Density dependence, harvest, and weather relations are well established from prior quantitative analyses (Houston 1982; Boyce 1991; Coughenour and Singer 1996; Boyce and Merrill 1996; Cheville et al. 1998; Singer and Mack 1999). This information was used to predict an “expected” elk population’s size and recruitment rate from 1995 to 1998 in the absence of wolves (Singer et al. 2002). The actual “observed” elk population following wolf restoration in 1995 was about 15% smaller and recruitment was lower (especially after 1997), strongly suggesting multiple predator limitation following the recent restoration of wolves (Singer et al. 2002; Fig. 1b), in concert with already existing predation on elk by coyotes, bears, and humans in the system (Singer et al. 1997).

### *The Biodiversity Approach*

Alternatively, a park manager’s measures in assessing ungulate abundance might focus on plant species, plant community, or other, diversity measures. Management of much of the world’s grazing land is based primarily on changes in plant species composition (Milchunas and Lauenroth 1992). In particular, dominant individual species have been used as indicators of range condition under the increaser-decreaser-invader concept. It has been suggested that ungulates in national parks should not be allowed to exceed levels that impact these diversity values (Wagner et al. 1995a; Berry et al. 1997). NPS (2001) policy also states that the natural abundance and diversity of plants and animals should be maintained within the bounds of natural processes.

In the biodiversity view, the trend in the relative amount of both plant community and plant species (i.e., richness, evenness) diversity is the measured variable. Disadvantages to applying this view are that responses of plant diversity to protection from ungulates (exclosures) or to new ungulate management programs may be long-term, on the order of one to many decades. Other confounding variables to ungulate herbivory, such as fluctuating beaver populations, climate change, succession, or hydrologic change, may also affect plant diversity and, thus, confuse the interpretations of any effects due exclusively to the ungulates. In addition, ungulates in pristine, natural ecosystems are known to alter plant species diversity in highly variable ways (McNaughton 1979; Pastor et al. 1993; Stohlgren et al. 1999). Research has demonstrated that ungulate grazing can alternatively decrease plant diversity (Rummell 1951; Chew 1982), result in no difference (Gough and Grace 1998; Stohlgren et al. 1999), or increase plant diversity (Grime 1973; Mueggler 1984). Ungulate effects on plant diversity may be variable in natural systems depending on environmental conditions, evolutionary history of grazing, and predator limitation (Collins and Barber 1985; Stohlgren et al. 1999). The basic tenet by some researchers that there should be no measurable effects of ungulates on plant diversity (Wagner et al. 1995a,b) has been questioned by others (McNaughton 1993, 1996). Management for maximum plant species diversity may, in some instances, include management for moderate, or even high, densities of ungulates. Thus, the grazing system and these major ecological relationships need to be well understood before managers can set goals for plant diversity.

### *The Grazing Optimization and Sustainability Approaches*

Measures to assess potential overabundance of ungulates might focus on their effects on plant production, sustainability and fertility of the ecosystem, and effects on ecosystem processes. These views assume that plants can respond to removal of aboveground tissues by ungulates through a number of compensatory responses and processes. In grassland grazing systems with native ungulates, less N is typically immobilized in litter and standing dead biomass (McNaughton 1983; Seagle et al. 1992), soil microbial biomass is likely decreased and, thus, net soil N mineralization is increased (Ruess and McNaughton 1987; Holland and Detling 1990; Frank and Groffman 1998). As a result, increased root uptake of N, increased N concentration in shoots, and increased N yield/unit tissue is often observed in herbaceous grassland plants grazed by native ungulates (Ruess 1984; Jaramillo and Detling 1988; Coughenour et al. 1990). The grazing optimization hypothesis has been observed at some moderate or low level of herbivory, where net primary production (NPP) is maximized and stimulated over ungrazed controls (McNaughton 1979, 1983, 1993; Dyer et al. 1993; Frank and McNaughton 1993; Turner et al. 1993; Green and Detling 2000). Compensatory responses in grasses enabled moderate levels of herbivory to be sustained (Biondini et al. 1998; Mazancourt et al. 1998). Several authors found no evidence for grazing optimization in grasslands (Verkaar 1992; Painter and Belsky 1993). Woody browse species may compensate for herbivory removals through increased number of branched shoots, increased size of regrowth shoots, and increased number of buds and number of long shoots (Bergström and Danell 1987). The central issue of this view is that providing plant production and soil fertility are maintained under grazing (McNaughton 1979, 1993; Frank and Groffman 1998), shifts in abundance of individual plant species or changes in biodiversity are of less concern. This view is useful to managers in that the end product, aboveground net primary production (ANPP), is a relatively straightforward and immediate measure to gather. Additionally, long-term productivity and sustainability is of paramount importance to ecosystem management. But sustained aboveground production under grazing may come at the expense of reduced root biomass, reduced seed production, or altered plant species abundance. These measures should also be sampled (Belsky 1986; Verkaar 1992; Painter and

Belsky 1993) and thus is an expensive and complex approach to apply. Managers must also decide how much effects due to ungulates on production, soil, and ecosystem processes are acceptable in a natural functioning system (see McInnes et al. 1992; Pastor et al. 1993), and that is a complex question to ask.

### *The Overgrazing Approach*

The overgrazing approach is the simplest approach that might be applied to a question of overabundance of an ungulate. Overgrazing is a value-laden term, but a term that is very simply defined as any excess of herbivory that leads to degradation of plant and soil resources. The challenge lies in defining what constitutes excess grazing since that definition is based on one's goals in managing an ecosystem. For example, a range manager, wildlife manager, or park manager might each define overgrazing differently (Coughenour and Singer 1991). In spite of these differences in opinion, there is some general agreement on what constitutes overgrazing of western rangelands. It is widely held, for example, that overgrazing results in reduced plant cover, increased bare ground, increased soil temperatures, drier soil, increased soil erosion, reduced organic inputs to the soil, and/or decreased plant productivity (Pengelly 1963; Westoby et al. 1989; Fuls 1992). Overgrazing also results in an increase in less palatable native plants, reduced size and vigor of plants, increased mortality of plants, invasion of perennial weeds, and eventually, invasion of annual weeds (Daubenmire 1940; Pengelly 1963; Westoby et al. 1989). These general criteria for overgrazing are relatively unambiguous. Thus, we feel the variables used in this view are relatively rapid and straightforward to sample, but the findings may be difficult to interpret. The challenge to the park manager is in deciding what constitutes "too much" of a grazing effect.

### *The Allowable Use Approach*

Perhaps the most commonly used approach in the western United States for evaluation of the appropriate number of ungulates focuses on allowable use levels on forages. First, aboveground net primary production (ANPP) is measured. A judgment is then made as to what level of use, or consumption, is allowable in that system and then the consumption level is sampled and monitored. For example, a level of 50% allowable use is often applied to livestock forage on western rangelands.

But effects on plants and processes of these proposed levels of allowable use have only rarely been quantitatively evaluated (see Biondini et al. 1998).

This approach is useful to managers since the measures needed to apply it reflect current conditions. The measure of interest, consumption rate, is an unambiguous measure of the direct interaction between a plant species and the ungulate herbivore. The view also lends itself well to adaptive management programs since new goals for consumption levels may then be set if expectations are not met.

Disadvantages of applying this approach are that measures of production and consumption are labor- and cost-intensive, and plant responses are highly variable to any specific level of use depending on the life form of the plant. Grazing system responses are influenced by the relative amount of underground root reserves, evolutionary history of grazing in a particular system, environmental conditions, and season of herbivore use (Milchunas et al. 1988; Frank and McNaughton 1992, 1993; Hamilton et al. 1998; Mazancourt et al. 1998).

We concluded from our review of a number of papers that reported consumption rates and effects on plants, that any allowable use values would be highly variable between ecosystems (Fig. 2a,b). We calculated a mean and variance level of use that appeared to be either: (a) sustainable, i.e., allowable; or (b) not sustainable, i.e., detrimental to plant production, fitness components, and continued abundance of the plant(s). Herbs and shrubs that grow in forest understories were the most sensitive to ungulate herbivory, followed by plants in grasslands with less evolutionary history of grazing (e.g., South American grasslands, Great Basin grasslands). Less sensitive ecosystems (e.g., the short-grass prairie or Serengeti grasslands) were those pre-adapted to herbivory through a longer evolution with ungulates, more prostrate growth forms of plants, and larger underground root reserves (McNaughton 1979, 1983; Milchunas et al. 1988). Shrubs were generally less tolerant of herbivory than grasses, probably due to few reserve meristems, nonintegrated modules, and slow, determinant growth (Whitham et al. 1991). Understory shrubs and trees that grow under shade in mature forests were less tolerant than seral shrubs that grow in strong sunlight that were characterized by rapid annual vertical growth rates (Fig. 2b).

## Study Objectives

The purpose of this investigation was to present a broad spectrum of data available from our research on

elk abundance and effects in RMNP and the adjacent town of Estes Park, Colorado, and compare this information to the criteria stated for each of the five different approaches. Elk were eliminated from the park in the late 1800's, reintroduced in 1913–1914, and artificially controlled by trapping in the park ecosystem by managers until 1968. Since 1969, the elk population has continued to grow and concerns over their possible overabundance have been expressed (Hess 1993; Berry et al. 1997). Our primary goal was to determine which of the stated criteria of the five approaches were the least ambiguous to sample, the easiest to apply to this case study, and the most closely aligned to NPS management policies and guidelines. We compared the operational clarity (i.e., the features of the approach that were specific, quantifiable, and readily measurable) and the time, cost, and potential management consequences of applying a particular approach to the case example.

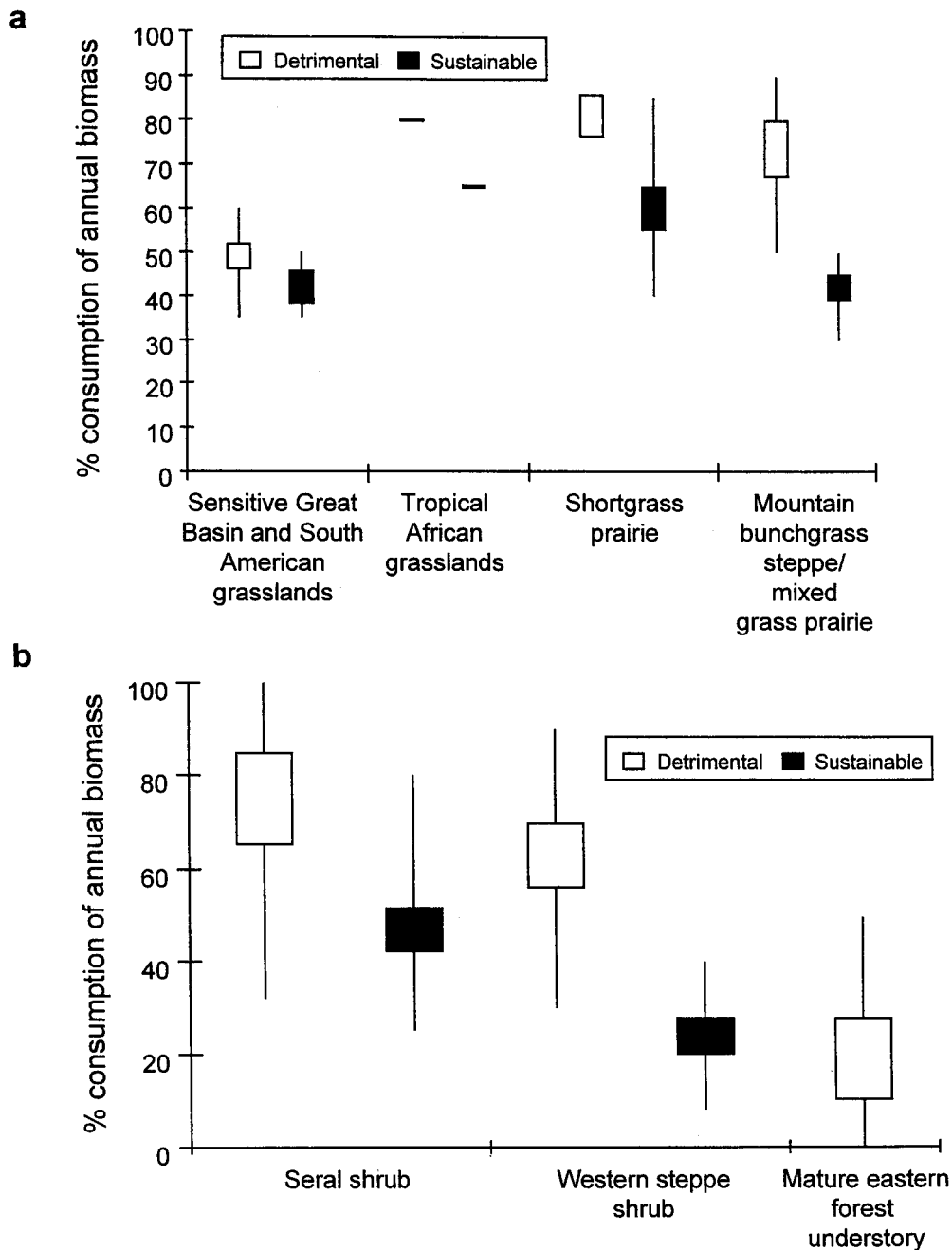
## Study Area

The low elevation elk winter range of RMNP encompasses approximately 17,000 ha in the upper montane zone along the eastern boundary of the park and the adjacent Estes Valley. Elk are free to move between protected national park land and the mix of public and private land in the Estes Valley. Glacial moraines running east-west divide the body of the park area into four major valleys, while the town of Estes Park lies in the middle of a broad park-like valley. Elevations in the study area range from 2,300 m at the lower end of the Estes Valley to 2,800 m on moraine ridge tops. Mean annual precipitation is 41 cm, most of it occurring as wet spring snows. An additional 2,000 ha of high elevation alpine tundra support a wintering population of approximately 125 animals.

## Methods

### *Population Analyses and Elk Concentrations*

Seventy-three elk were radiocollared in January 1995 and monitored by ground and aircraft until 1998 (Larkins 1997; T. L. Johnson, RMNP, unpublished data). We divided the winter range into four logical sectors based on movements of radiocollared elk (Fig. 3). We estimated the total size of each sector and the area of each vegetation cover type in each sector (Appendix A) using geographic information systems (GIS). All elk



**Fig. 2.** Schematic of percent consumption of herbaceous (a) and shrub (b) species by ungulates that were reported in the literature to be sustainable or detrimental to growth, production, vigor or fitness components. Grassland Sources (a) include: Daubenmire (1940); Rummell (1951); Klippe and Costello (1960); McNaughton (1979, 1983); Hilbert et al. (1981); Mack (1981); Sneva et al. (1984); McLean and Wikeem (1985); Rickard (1985); Sala et al. (1986); Jaramillo and Detling (1988); Milchunas et al. (1988); Polley and Detling (1988); Frank and McNaughton (1992); Fuls (1992); Seagle et al. (1992); Singer and Harter (1996); Olson and Wallander (1997); Biondini et al. (1998); Frank and Groffman (1998); and Pucheta et al. (1998). Shrub Sources (b) include: Aldous (1952); Krefting et al. (1966); Willard and McKell (1978); Wolff and Zasada (1979); Oldemeyer (1981); Wolfe et al. (1983); Danell and Bergström (1985); Bergström and Danell (1987); Wagstaff and Welch (1991); McInnes et al. (1992); Pastor et al. (1993); Singer and Renkin (1995); Singer et al. (1994); and Ritchie et al. (1998).

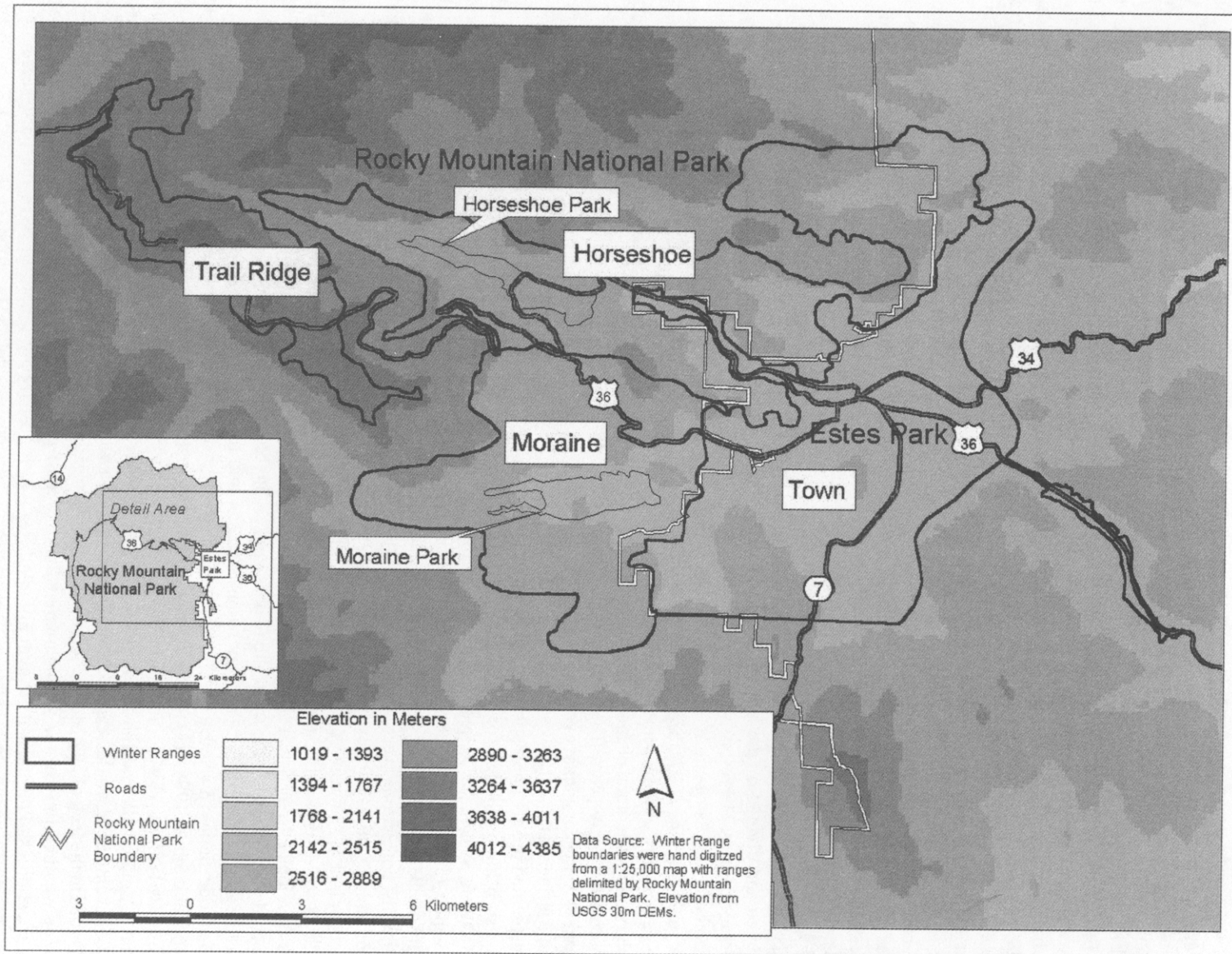


Fig. 3. Map of winter ranges of elk in Rocky Mountain National Park, Colorado.

radiolocations were plotted and digitized and each radiocollared elk was classified as to the sector in which it spent each season (town, Moraine, Horseshoe, Trail Ridge ranges). Winter elk density was calculated using data from 6 years of annual aerial surveys (F. J. Singer, unpublished data). The surveys concentrated on Horseshoe and Moraine Parks, and were not flown over the town of Estes Park or Trail Ridge Range. The surveys were flown seven times during the 6 years on March 9, 1994; February 14, 1995; December 15, 1995; February 11, 1996; February 19, 1997; March 12, 1998; and February 13, 1999. Elk density was calculated for each survey based on a grid with 100 m cell size and a 3,000 m search radius using the ArcView 3.1 GIS density calculation function. We used a kernel density method, which distributes the group size information from the observed group location and, therefore, results in a smoother density gradient. The total number of elk within 3,000 m of each cell was calculated and divided by the search area to find the density of the cell. All density grids were then summed and divided by the number of surveys to get an average density. The results were then mathematically smoothed. Elk distributions varied little between the study years (Larkins 1997), probably because snow depths were typically shallow across most of the winter range in the study winters and depths did not vary greatly, at least during the study years. Thus, we feel these values accurately represent annual average elk activity and elk grazing influences.

We estimated the elk population size in the park by recording sighting variables for each group of elk observed during systematic helicopter surveys of the primary winter range. The effect of these variables on sightability of elk was tested using radiocollared elk and the sightability corrections were used to estimate the number of animals missed following the methodology of Samuel et al. (1987), Unsworth et al. (1994) and this study. Elk in town were estimated from mark-resight estimates developed from repeat surveys each winter. We compared the potential of the town and park sectors to support elk using three methods: (1) population-based estimates of food-limited  $K$  (Houston 1982; Boyce 1993; Coughenour and Singer 1996); (2) forage-biomass based estimates (Holzgang 1997); and (3) forage and nutritional estimates of food-limited  $K$  (Hobbs et al. 1982). We assumed elk would reach food-limited  $K$  in the sectors due to the lack of evidence for any substantial predator or weather limitation. We compared these potential capabilities to the current estimates of elk that exist in the sectors using the aerial sightability estimates in the park and ground mark-resight estimates in town.

Data to estimate population size, age and sex composition, and survival rates were intermittently available for elk populations in RMNP from 1965 to 2001. Similar data were available for elk outside the park, in the Estes Valley, from 1979 to 2001. A population-projection model incorporating density dependence and weather covariates was developed and fit to the available population data in both the park and the town sectors. Model fitting was accomplished by minimizing the sum of squared errors between model estimates and direct estimates weighted by the inverse variances of each direct estimate, following Lubow et al. (this volume).

In the population model, both calf survival,  $S_c$ , and recruitment (similar relationship, not shown) for each population is related to density and four weather statistics through a logistic model:

$$S_c = \text{LOGIT}(\beta_0 + \beta_1 N_T + \beta_2 \bar{T}_S + \beta_3 \bar{T}_W + \beta_4 \bar{P}_S + \beta_5 \bar{P}_W)$$

where  $N_T$  is the total population size,  $\bar{T}_S$  and  $\bar{T}_W$  are average summer (April–August) and winter (September–February) temperature deviates,  $\bar{P}_S$  and  $\bar{P}_W$  represent average summer and winter precipitation deviates, and the  $\beta$  values are estimated parameters. LOGIT represents the logistic function:

$$\text{LOGIT}[f(x)] = \frac{1}{1 - e^{-f(x)}}$$

Alternative population models were considered and the best one selected using Akaike's Information Criteria ( $AIC_c$ ). The smallest  $AIC_c$  values represent best biological models since the  $AIC_c$  statistic corrects for additions to the number of parameters (Burnham and Anderson 1992).

A second, independent food-based estimate of  $K$  in town was calculated following the methods used in the Swiss National Park (Holzgang 1997). This method involves using calculations of available forage, offtake, and forage requirements to estimate ungulate numbers. We used a 1996 Spot satellite image, with 10 m panchromatic and 20 m multispectral resolution to classify vegetation types for the elk winter range in the town of Estes Park, Colorado (Appendix B). Vegetation was stratified into open grasslands, pine grasslands, wet meadows, irrigated and slightly sub-irrigated grasslands, golf courses, disturbed grasslands, and forested types. A food-based estimate of  $K$  in the park sector was previously calculated by Hobbs et al. (1982). Total forage biomass was sampled (see "Allowable Use Measures"

below) and corrected for available forage using a GIS with vegetation data (Appendices A and B). The total available forage biomass for elk was adjusted for sampled offtake values and divided by the forage required per elk for the 7-month winter use of the town range to arrive at  $K$  for the town. We predicted forage use would average 50–55% over the landscape based on observed use of forages by elk near  $K$  in the park (57% offtake) and near Maybell, Colorado (60% offtake, Hobbs 1996). We estimated average forage use across the landscape in town would be less than the park or Maybell examples due to some elk-proof fences, other human structures that blocked elk, and avoidance of some core subdivision lawns where elk use was restricted. We did not calculate how much of these town areas were inaccessible to elk, but we feel this lower range of use levels approximates the maximum average use level that might occur in town. We assumed the average elk consumption was 5 kg dried forage per day (Hobbs 1979). We calculated the average number of days elk spent in the town winter range ( $\bar{x} = 210 \pm 7$  days) from 30 radiocollared elk over four winters to arrive at a mean of 1,050 kg forage consumed per elk per winter in town.

We also inspected the extent of any possible artificial concentrations of forages for elk in town by calculating the N yield in the fertilized and irrigated grassland types in town sampled in 1997–1998 and comparing that to the N yield from undisturbed grasslands in the town sector. Nitrogen yield was estimated as the concentration of N in forages multiplied by the peak standing crop biomass of forages. We also used GIS to estimate the areas of grasslands lost to human modifications (impoundments, buildings, and pavement) and GIS combined with groundtruthing to estimate the grassland areas that were improved due to human modifications (golf courses, irrigated pastures). From this, we projected an elk  $K$  for the town sector under pristine conditions. We present carrying capacity estimates for dry years, since those are years of critical minimums, and for average years, since the elk population will be most likely to track average forage conditions.

### *Vegetation Sampling Locations*

Sixteen study sites were randomly selected in 1994 for placement of grazing exclosures (46 x 30.5 m) and paired grazed plots, in the elk winter range in the montane riparian and upland shrub communities of northeastern RMNP. Vegetation communities were identified and random points generated in the appropriate vegetation type using GIS. Twelve exclosure

study sites were located in riparian willow communities of the Moraine Park area of the Big Thompson River drainage (elevation 2,481 m) and the Horseshoe Park area of the Fall River drainage (elevation 2,598 m). An additional 25 willow study locations in grazed sites throughout the park winter range were randomly selected using GIS and sampled in 1996. Four study sites were located in upland shrub/grassland sites. These sites were all located on southern exposures in the areas of Hallowell Park, Deer Ridge, Aspenglen Campground, and the Beaver Meadows Entrance Station.

Predominant willow species throughout willow areas were *Salix monticola*, *S. planifolia*, and *S. geyeriana* mixed with other wet site shrubs such as *Potentilla fruticosa*, *Betula glandulosa*, *B. occidentalis*, and *Alnus tenuifolia*. We selected willow communities for intense study because willow (*Salix* spp.) was suspected to be a significant diet component for elk (D. Stevens, personal communication; Hobbs et al. [1981]) and willows are not rare--willow communities comprise about 4% of the total winter range and 30% of the core elk winter range. We did not want to monitor a rare vegetation type, since rare plants or rare plant communities may not respond in linear fashion to elk densities and there may be no feedback. We also recognized a short willow type that constituted about 70% of the willow communities and a tall willow type that constituted 30% (Peinetti et al., this volume). Both types were sampled proportionately. Eight of the willow exclosure sites (four in Moraine Park and four in Horseshoe Park) were located in areas that had previously held beaver dams but had little or no current beaver activity, that had dewatered channels, and that supported short, heavily browsed willow. In all of these "short willow" sites, evidence from dead and decadent willows indicated that plants over 2 m tall were once present. The other four willow exclosures sites (two in Moraine Park and two in Horseshoe Park) were located in beaver-occupied areas (including areas of recent activity), that supported taller willow plants subject to less severe hedging by the elk that we referred to as "tall" willows.

Primary vegetation cover of the upland shrub/grassland type consisted of antelope bitterbrush (*Purshia tridentata*) and mountain muhly (*Muhlenbergia montana*) associated with sparse ponderosa pine (*Pinus ponderosa*).

Three pre-existing, longer-term exclosures were placed in a mixture of big sagebrush (*Artemisia tridentata*), wet meadow, and aspen (*Populus tremuloides*) vegetation types in 1963 in the Beaver Meadows drainage. These sites had not been randomly



located. Grazed and ungrazed sites were also sampled at these exclosures.

Vegetation sampling in the town sector consisted of 14 sampling sites within six vegetation types sampled in 1997 through 1998. The vegetation/habitat types chosen reflect areas where elk are most often observed grazing in winter. Six sites in three additional vegetation types were chosen and sampled in summer 2000.

### *Elk Density Correlates to Willow Growth--Grazing Optimization*

To test our assumption concerning the relative importance of willow in elk diets, 55 fresh elk fecal samples were collected on low elevation winter ranges in November 1994 and 1995; February 1995; and April/May 1995–1997. Samples were also taken on alpine summer range in the spring of 1995 and the summers of 1995–1997. Each sample was a composite of 8–10 fecal pellets from 8–10 individual elk in a group. Samples were frozen until immediately before processing, and then dried at 55°C for 48 hours before shipping to the Composition Analysis Laboratory in Fort Collins, Colorado. Samples were ground together and three subsamples taken from each sample for analysis. The dietary components in each subsample were identified to genus. Then the subsamples were pooled to determine average percentage contribution to total diet for that sample.

Twenty-five willow sample sites were randomly selected from within all mapped willow types on the winter range using GIS procedures and sampled in 1996. The following variables were measured on three to five circular subsample plots, each 9.3 m<sup>2</sup> in size, at each willow sample site: average shrub height (cm), maximum shrub height (cm), stem density (stems/ha), shrub density (shrubs/ha), twig production (kg/ha), total new shoot production or current annual growth (CAG; kg/ha), canopy volume (m<sup>3</sup>/ha), and canopy cover (m<sup>2</sup>/ha). The data were recorded for 3 willow species (*Salix monticola*, *S. planifolia*, and *S. geyeriana*) from the 25 plots as well as the 12 grazed plots paired to the willow exclosures in Moraine and Horseshoe Parks. The variables from the subsample plots at each location were averaged and pooled across willow species. Only this single mean was entered, since the subsamples of plots at a location were not independent of each other. Of these willow sample sites, 31 had enough information to be assigned to a category of average 1994–1999 elk density from the mapping effort. At the grazed plots paired to the 12 exclosure sites, consumption rates were calculated for 3

years (1995, 1996, and 1998). A single mean depth to the water table for the month of June, the time of most of the annual growth of willows, was also averaged from three water wells at each of these 12 sites for 3 years.

The effects of elk density, elk consumption of willows, and depth to the water table on the eight willow size and growth variables were inspected using linear regression. The CAG, stem density, plant density, twig production, shrub volume, and shrub area measures were log-transformed. Akaike's Information Criteria corrected for small sample size (AIC<sub>c</sub>) was used to evaluate the best, or most parsimonious models:

$$AIC_c = \frac{\ln(SSE)}{n} + \frac{n + K}{n - K - 2}$$

where SSE = sum of squares error and  $K$  = number of parameters (Burnham and Anderson 1992; McQuarrie and Tsai 1998). The AIC<sub>c</sub> process provides a quantitative measure for the trade-off between the increased precision achieved by adding additional variables to the statistical models versus the "cost" to the parameter estimation of adding a variable. The lowest AIC<sub>c</sub> values for a well-designed biological model indicate the "best" and most parsimonious model of the choices tested (Burnham and Anderson 1992).

Any threshold values in elk density or elk consumption rates that influenced willow size and growth variables were also inspected. The approximate threshold of elk density at which the willow growth variables were reduced 40% from peak values and to levels below ungrazed values, were identified using a line fit to the points using Friedman's smoothing method (S-plus 2000). A judgment was made that this threshold constituted a biologically important decline in willow growth. Any potential grazing optimization, or peak aboveground production that might be observed at moderate levels of ungulate consumption rates, was identified.

### *Effects of Elk on Plant Species Diversity*

The Shannon-Weaver diversity index (Shannon and Weaver 1962) and species richness index ( $R$ ) were calculated for 0.25-m<sup>2</sup> herbaceous plots sampled in the park, and then averaged across plots at each site to determine the average index value for species diversity and richness for each treatment (Appendix C). We tested for differences in diversity indices between grazed and ungrazed sites using non-parametric statistical analysis.



An analysis of variance of ranked data for each index in each vegetation type was conducted, as well as a Wilcoxon rank test. These indices were computed using all plant species without regard to whether plants were exotic or native. ANOVA tests of abundance of each individual species between grazed and ungrazed treatments were also conducted. We categorized plants into native and exotic species and then compared total production of natives and exotics between grazed and ungrazed sites with PROC MIXED, an analysis procedure that is a generalization of the standard linear model design using SAS (statistical analysis software) v6.12. PROC GLM, the general linear model for data with only one source of variation, was used for data analysis from upland grass/shrub sites and the F-protected least significant difference was used to determine significant differences between means.

### *Grazing Sustainability or Optimization Measures*

Three 9.3 m<sup>2</sup> circular plots were established in each exclosure and grazed site to measure shrub production. Data on shrub production were collected in late summer of 1994–1996 and 1998 for willow sites and 1994–1997 for bitterbrush sites (Zeigenfuss et al., this volume). Data collected on each plant included species, canopy diameters (widest and perpendicular to widest diameter), plant height, number of stems, and estimate of percent of canopy that was dead. Regression equations were developed for prediction of production for the three major willow species and bitterbrush. Equations were developed separately for Moraine and Horseshoe Parks for 1995 and 1996. Then a pooled equation was developed and used to predict total willow production for 1994 and 1998. R<sup>2</sup> values for these equations were high and ranged from 0.75 to 0.92. Samples were taken from the 35-year exclosures following the same methods in 1998 and 2000.

Herbaceous standing crop biomass data were collected by clipping three to five randomly located 0.25 m<sup>2</sup> circular quadrats in late summer 1994 at each exclosed and grazed site. All graminoids and forbs within the quadrat were clipped and sorted by species to measure annual peak standing crop. Litter was also collected from within each quadrat. Vegetation was oven dried at 55°C for 48 hours and then weighed. Visual estimates of percentage bare ground, moss, lichen, cacti, and shrubs were

also recorded. Town sample sites in subirrigated wet meadow, slightly subirrigated wet meadow, cattle grazed, ponderosa pine/grasslands, upland grasslands, and disturbed grasslands were sampled in July 1997 and 1998 (average precipitation years). Golf course sites were sampled in late November 1997 after mowing ceased. The wet meadow sites and disturbed grasslands were also sampled in July 2000 (a dry year). Subirrigated wet meadow sites were compared between average and dry years to determine a scale factor for biomass production between different precipitation years. This scaling factor was applied to the forage-based model used for estimating elk *K* in town. Methods follow those listed above with the exception that samples were grouped into graminoids and forbs. Predominant species were noted for purposes of comparison of sites. All vegetation types at the 35-year exclosures were similarly sampled in August 1998.

Several willow individuals ( $n = 2\text{--}4$ ) of the three predominant species (*Salix monticola*, *S. planifolia*, and *S. geyeriana*) in each treatment at each exclosure were also tagged for more intensive measurement throughout the course of the study. Samples for nutrient analyses were obtained from these tagged willows in August 1998 and January 1999. Composite graminoid and forb samples from the previous growing season were collected from plots subjected to elk herbivory in April 1998 (all sites). Composite samples from current graminoid and forb growth were collected in July 1997 (bitterbrush sites) and 1998 (willow) from all treatments. Samples were analyzed for carbon (C) and N content using a LECO CHN-1000 Carbon Hydrogen and Nitrogen Analyzer. Dried and ground plant samples were combusted in a chamber and resultant gases passed through infrared cells to determine C and through a thermal conductivity cell to determine N.

Root samples were collected using a 6.35 cm diameter root corer driven 20 cm into the soil inside and outside of all 4-year exclosures in 1996 and 1999 and 35-year exclosures in 1999. Roots were refrigerated ( $\sim 4^\circ\text{C}$ ) until they were processed. Processing of samples consisted of washing to remove soil from roots then drying them in a forced air oven at 55°C for at least 48 hours. Dried root samples were brushed to remove any remaining large particles of soil and then sorted into coarse ( $>2\text{ mm}$ ) and fine ( $<2\text{ mm}$ ) components. Dried root samples were then weighed to the nearest 0.0001 g and analyzed for percent total N as described above. A subsample of the roots was weighed, combusted in a

muffle furnace at 550° C for 6 hours, then weighed again to determine the percent organic matter, based on the ash sample. The actual root biomass weight was then determined by multiplying the percent organic matter by the weight of the entire dried root sample.

### *Allowable Use Measures*

Five 9.3 m<sup>2</sup> circular plots were measured in areas subjected to elk herbivory at each exclosure site to estimate shrub consumption by ungulates following the general methods described above. Winter use was measured before leaf bud break in May, and summer use was measured in August, 1994–1998. On every fourth individual of each species, a subsample of the number of browsed and unbrowsed leaders, and twig basal, tip, and browse diameters were also collected. Percent leader use was determined using the equation:

$$\% \text{ leader use} = \frac{a}{a + b}$$

where  $a$  = number of browsed leaders and  $b$  = number of unbrowsed leaders. Average percent twig removed was determined using the method of Jensen and Urness (1981) and Pitt and Schwab (1990) following the formula:

$$\% \text{ twig use} = \frac{100(D_p - D_t)}{D_b - D_t}$$

where  $D_p$  = twig diameter at point of browsing,  $D_t$  = diameter of a representative sample of twig tips, and  $D_b$  = basal diameter of current year's twig growth. Total consumption was determined by multiplying % leader use by % twig use.

Six grazing cages were randomly placed at each grazed plot for measurement of winter herbaceous consumption. Paired 0.25 m<sup>2</sup> plots inside and outside these cages were clipped in spring, prior to greenup. Cages were randomly relocated after the spring sampling to capture the early summer consumption that occurs during elk migration to summer ranges. Vegetation collected inside and outside these grazing cages was dried at 55° C in a forced air oven for 48 hours and then weighed. Percent consumption was calculated using the following formula:

$$\% \text{ consumption} = \frac{100 * (B_i - B_o)}{B_i}$$

where  $B_i$  = dry weight of biomass inside grazing cage, and  $B_o$  = dry weight of biomass outside of the grazing cage.

Town sites, except the golf course, were sampled for winter offtake in March and April 1998, and spring-summer offtake in July 1998. Methods follow those listed above. Percent biomass consumed was compared between vegetation/habitat types for each sample period using analysis of variance methods.

All analyses of plant measures were performed using SAS (version 6.12) statistical software. Shrub and herbaceous production and consumption data from willow sites were analyzed for differences between grazed and ungrazed treatments using PROC MIXED. PROC GLM was used for analysis of data from upland grass/shrub sites and the F-protected least significant difference was used to determine significant differences between means. The variables of willow growth were log-transformed to stabilize variance.

### *Potential Overgrazing Measures*

We sampled percent bare ground in 30 grazed and ungrazed plots at five paired locations at the 35-year exclosures in 1998 and at the 4-year exclosures. Bulk density and percent organic matter for the paired plots were sampled by Binkley et al. (this volume) and Menezes et al. (2001). Cover and biomass of herbaceous plants were sampled on three 0.25 m<sup>2</sup> plots at each grazed and ungrazed site. The effects of grazing on individual plant species and all plant species pooled were compared using ANOVA methods.

## **Results**

### *Elk Population Analyses and Potential Overconcentrations*

The radiocollared elk were classified as either town or park animals based on criteria of >65% of winter locations in one sector or the other. Sixty-two radiocollared elk spent the winter in either: (a) town, (b) the Horse-shoe Park area, or (c) the Moraine Park and Beaver Meadows complex, and rarely moved among these three sectors. Eleven other radiocollared animals were classified as wanderers and moved freely among the town and park sectors. The Trail Ridge winter range only supports 100–125 animals and was not included in the plant studies, although the area is also a significant summer range for migratory elk.

Population-based estimate of food-limited  $K$  for the park sector of the elk population was  $1,069 \pm 55$  ( $\bar{x} \pm \text{se}$ ) animals (Table 1). The park sector of the elk population was at or near this level for about the last 10–13 years prior to the analysis (during which time  $\lambda$ , or population growth, leveled off and approximated 1.0). Colder winter temperatures were correlated with reduced calf recruitment (calves:cow at age 0.5 yrs) and with reduced calf survival (between age 0.5 to 1.5 years) in town. Recruitment of town elk also increased with warmer summer temperatures and greater summer precipitation. No weather covariates were significantly correlated with calf recruitment or survival in the park. Declining calf recruitment has been nearly linear and similar in both the park and town. However, density response of calf survival in the park was abrupt near carrying capacity and has not yet been detected in town, suggesting that this mechanism of density dependence is difficult to detect until the population is near carrying capacity. Forage-based food-limited  $K$  for the park sector was estimated by Hobbs et al. (1982) as  $991 \pm 102$  in a dry year and  $1,481 \pm 261$  in a wet year. Since Hobbs et al. (1982) only had estimates for years 40% wetter and 20% drier than average, we calculated an average precipitation year estimate by weighting the dry year estimate by twice that of the wet year (because it was twice as close to average). The resulting average precipitation year estimate of forage-based  $K$  in the park for elk was  $1,154 \pm 163$  elk.

Population-based estimate for potential food-limited  $K$  for elk in the town sector was estimated at about  $2,869 \pm 415$  elk, or well above the current (2001) average numbers of about  $1,975 \pm 150$  elk estimated in the town sector. This sector of the population has recently grown as rapidly as 11.0% per year, and is most recently growing at 5.2% per year (1991–2001). Under average precipitation, the forage-based estimate of food-limited  $K$  for elk in the town sector ranged from  $3,082 \pm 103$  to  $3,391 \pm 113$  elk if consumption rates were 50–55%. This level of consumption was close to the average level measured in upland and willow areas in the park where elk exist at food-limited  $K$ . However, due to lowered plant production in dry years, forage-based estimate of food-limited  $K$  for elk in town dropped to  $2,330 \pm 78$  to  $2,563 \pm 85$  during a dry year. Population-based estimate of food-limited  $K$  for the entire elk population (both town and park) was estimated at  $3,938 \pm 419$  elk ( $2,869 \pm 415$  in town,  $1,069 \pm 55$  in the park).

Elk densities were variable in the park and were observed to be high (30–65 elk/km<sup>2</sup>) to very high (66–110 elk/km<sup>2</sup>) on about 7% of the park's winter range. The high elk concentration areas were almost exclusively in Moraine Park (Fig. 4). Elk densities were much lower, <10 elk/km<sup>2</sup>, on the remaining 82% of the park primary winter range. Average elk density in the entire town sector was higher than overall density in the park sector (Fig. 4). Density of elk in town averaged approximately 28.5 elk/km<sup>2</sup>. This is, no doubt, due to the larger total

**Table 1.** Comparison of three different estimates ( $\bar{x} \pm \text{s.e.}$ ) of potential food-limited  $K$  and current population estimates for elk in Rocky Mountain National Park (park sector) and the adjacent town of Estes Park (town sector), Colorado.

	Elk population sector	
	Park	Town
Food-limited $K$ : the potential to support elk		
Population-based, from growth trajectories		
park 1965–1999, town 1988–1999	$1,069 \pm 55$	$2,869 \pm 415$
Forage biomass or nutrition-based (1997–2000)	$1,154 \pm 163$	$3,082 \pm 103$
Population estimates (2001)	$1,074 \pm 39^a$	$1,975 \pm 150^b$

<sup>a</sup>Based on aerial sightability (1995–2001).

<sup>b</sup>Based on ground mark-resight (1995–2001).

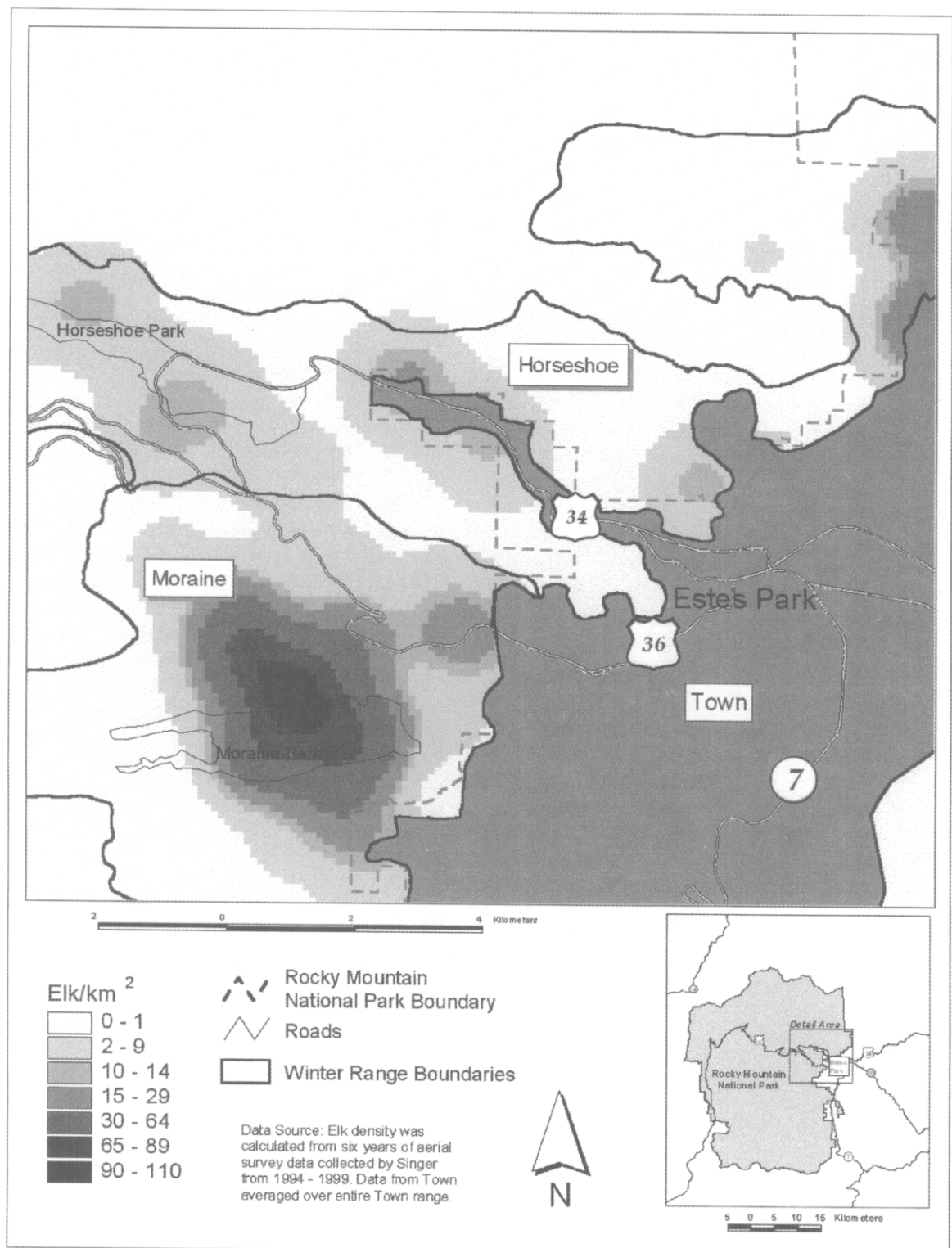


Fig. 4. Elk densities (elk/km<sup>2</sup>) on winter range in Rocky Mountain National Park, Colorado, 1994–1999.

amount of grassland types in town (28.4 km<sup>2</sup>) compared to total grasslands in the park sector (15.0 km<sup>2</sup>). In addition, the town sector is about 100 m lower in elevation and has less snow in winter than the park sector. Biomass production and N yield on some irrigated and fertilized grasslands in the town sector also provide an unnaturally higher concentration of forage on those sites (Fig. 5).

The human improvements to the managed golf course and pasturelands (fertilization, irrigation) resulted in increased nitrogen yield in forages on those sites and nearly compensated for the complete loss of 0.47 km<sup>2</sup> of elk winter range to the Estes Lake impoundment and 1.05 km<sup>2</sup> to buildings and pavement. At 50% consumption rates, we estimated that  $3,251 \pm 109$  elk could have been supported under average precipitation conditions in the town sector under pristine conditions, and that  $3,082 \pm 103$ , or about 5% fewer, elk can potentially be supported under these current human-altered conditions in the town sector. Under lower forage production during dry years, we estimated that  $2,330 \pm 77$  elk could be supported under current modified conditions, and  $2,424 \pm 81$  elk under pristine conditions.

### *Correlation of Elk Density to Willow Growth*

Graminoids were the most important diet component (71%) during winter and spring, when elk made significant use of the park's winter range. All trees and shrubs combined comprised 22% of fall-winter-spring diets on the winter range. Willows (*Salix* spp.) comprised 11.7% of the elk diets during all three seasons when elk spent some time on the winter range (Appendix D).

Average winter elk density, 1994–1999, was negatively, but weakly, correlated to willow size, density, and production measures ( $P < 0.10$ ; Table 2). For the 12 willow sites sampled during all 3 years, and where depth to the water table was also included as a covariate with elk density, there was also a significant negative correlation between elk density and willow size, stem density, and production measures, but not to total shrub density ( $P = 0.87$ ). AIC<sub>c</sub> values indicated the best model included both elk density and depth to water (Table 2; Fig. 6). We found elk density to be positively correlated with higher water tables on some of our study sites (those in Moraine Park;  $R = 0.44$ ,  $P = 0.01$ ). Moraine Park was also the location where a negative relationship between water table levels and willow production and height was found. This indicates that any positive effects of higher water tables on willow production may be offset by the

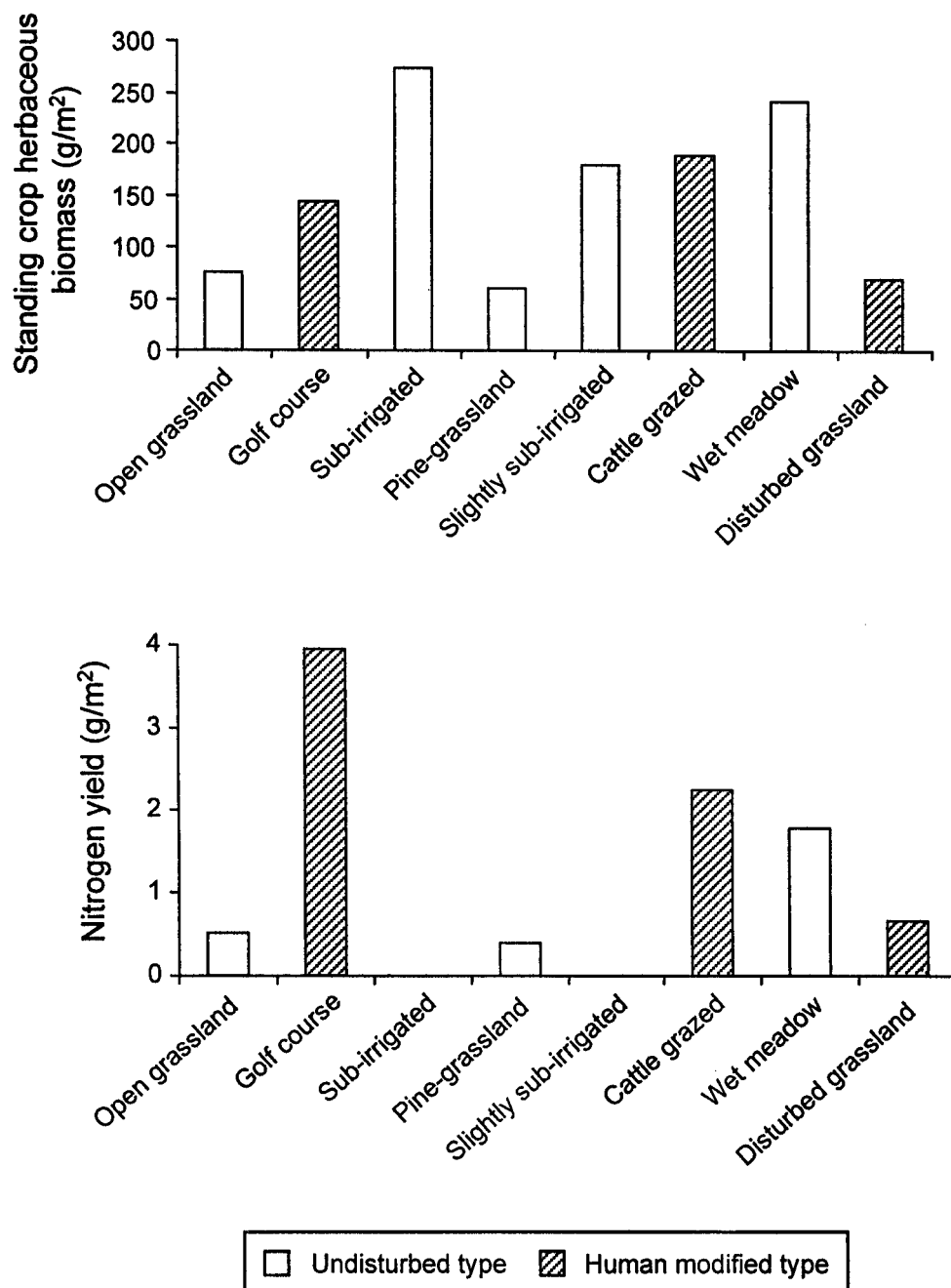
suppressing effects of high elk density on willow growth. In Horseshoe Park, where elk densities were lower overall, the water table level was positively correlated (though not significantly) with willow production and height, as well as herbaceous production. We concluded from these models that elk density had a much greater influence on willow growth in this study area than did depth to the water table. We also noted there were higher, although not significant, average elk densities in the short willow ( $30 \pm 6$  elk/km<sup>2</sup>) versus the tall willow type ( $24 \pm 10$  elk/km<sup>2</sup>;  $P = 0.68$ ).

Elk consumption rates of willow were positively correlated with elk density ( $P = 0.003$ ;  $r^2 = 0.495$ ). The best fit ( $r^2$  values) for the relation of elk consumption rates of CAG of willows to willow sizes and growth was slightly greater using a second order model that included the independent variable of consumption, consumption<sup>2</sup>, and depth to the water table (Table 2). The lowest AIC<sub>c</sub> values, however, suggested the best model included a second order model with consumption only and not depth to the water table (although the AIC<sub>c</sub> differences between the two models were small and biologically insignificant—only two AIC<sub>c</sub> points—indicating water was potentially important). This curvilinear relationship to rates of consumption strongly suggested grazing optimization and a peak in willow growth at moderate levels of elk consumption ( $\bar{x} = 21 \pm 0.4\%$  annual consumption of willow CAG), but a subsequent negative influence on willow growth at higher rates of consumption ( $\geq 37\%$  consumption; Fig. 7). The smoothed relationship identified the approximate elk density of  $\geq 32 \pm 1$  elk/km<sup>2</sup> and elk consumption rate of  $\geq 37 \pm 3\%$  removal of willow as the threshold levels where our criteria of a 40% decline in most components of willow growth from maximum growth levels occurred (Figs. 6 and 7).

Shrub CAG, willow canopy volume and area, and annual shoot growth of willows were all best explained (i.e., the lowest AIC<sub>c</sub> values) by the second order model of elk consumption rates, while average willow height, maximum height, and stem and shrub densities were best explained by models that included both elk density and depth to the water table (Table 2).

### *Effects of Elk on Plant Species Diversity*

Elk herbivory did not have a consistent effect on plant species diversity across vegetation types. However, species richness was greater in ungrazed plots in short willow sites in 1995 than grazed plots in the same year, but this difference was not quite significant ( $P = 0.15$ ;



**Fig. 5.** Production and N yield ( $\text{g/m}^2$ ) of herbaceous forage of select common human disturbed and undisturbed vegetation types in the town of Estes Park, and inside Rocky Mountain National Park, Colorado. Some values for N were not available.

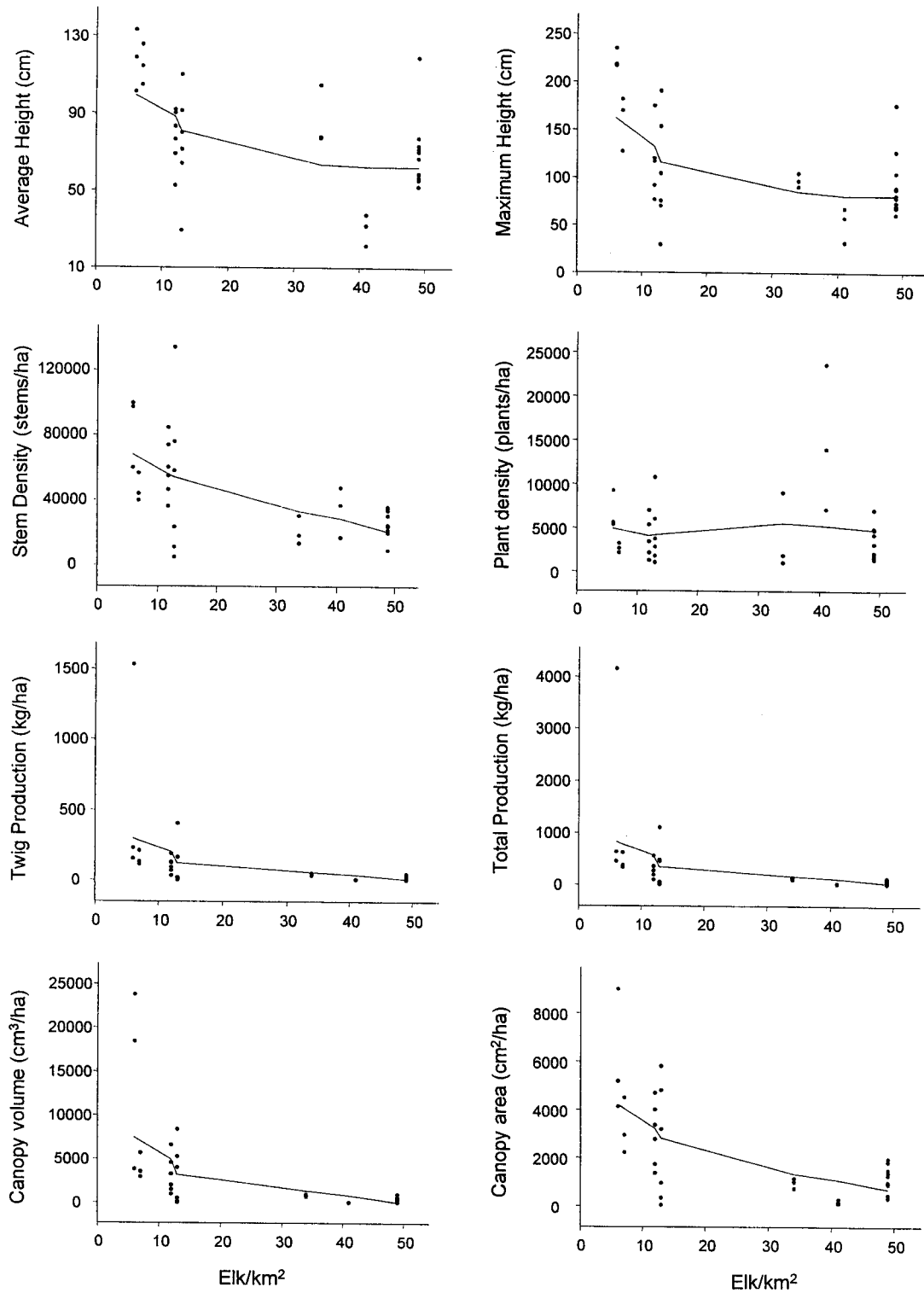
**Table 2.** Model of independent elk density and consumption variables on willow size, density, and growth (dependent) variables in Rocky Mountain National Park, 1994–1998.

Dependent variables	Elk density, 1994–1999 vs. landscape sites sampled in 1996 (n = 31)	Elk density alone 1994–1999 (n = 35)	Elk density and depth to the water table (n = 35)	Elk consumption, consumption <sup>2</sup> (n = 35)	Elk consumption, consumption <sup>2</sup> , and depth to the water table (n = 35)
Total current annual growth (CAG)					
$r^2 =$	0.111	0.409	0.46	0.466	0.467
F =	3.62	7.14	6.34	13.98	9.08
P =	0.07	0.0009	0.0008	0.0001	0.0002
AIC <sub>c</sub> =	1.95	1.30	1.26	1.27	1.35
d.f. =	30	34	34	34	34
Average willow height					
$r^2 =$	0.0005	0.495	0.548	2.656	0.274
F =	0.02	10.12	9.08	5.79	3.98
P =	0.90	0.0001	0.0001	0.007	0.018
AIC <sub>c</sub> =	9.86	7.13	7.09	7.57	7.67
d.f. =	30	34	34	34	34
Maximum willow height in plot					
$r^2 =$	0.007	0.511	0.604	0.25	0.257
F =	0.21	10.79	11.44	5.37	3.57
P =	0.65	0.0001	0.001	0.010	0.025
AIC <sub>c</sub> =	10.63	8.40	8.25	8.89	8.96
d.f. =	30	34	34	34	34
Willow stem density/plot					
$r^2 =$	0.277	0.266	0.376	0.25	0.26
F =	11.13	3.74	4.53	5.35	3.64
P =	0.002	0.021	0.006	0.010	0.023
AIC <sub>c</sub> =	0.58	0.21	0.12	0.29	0.37
d.f. =	30	34	34	34	34

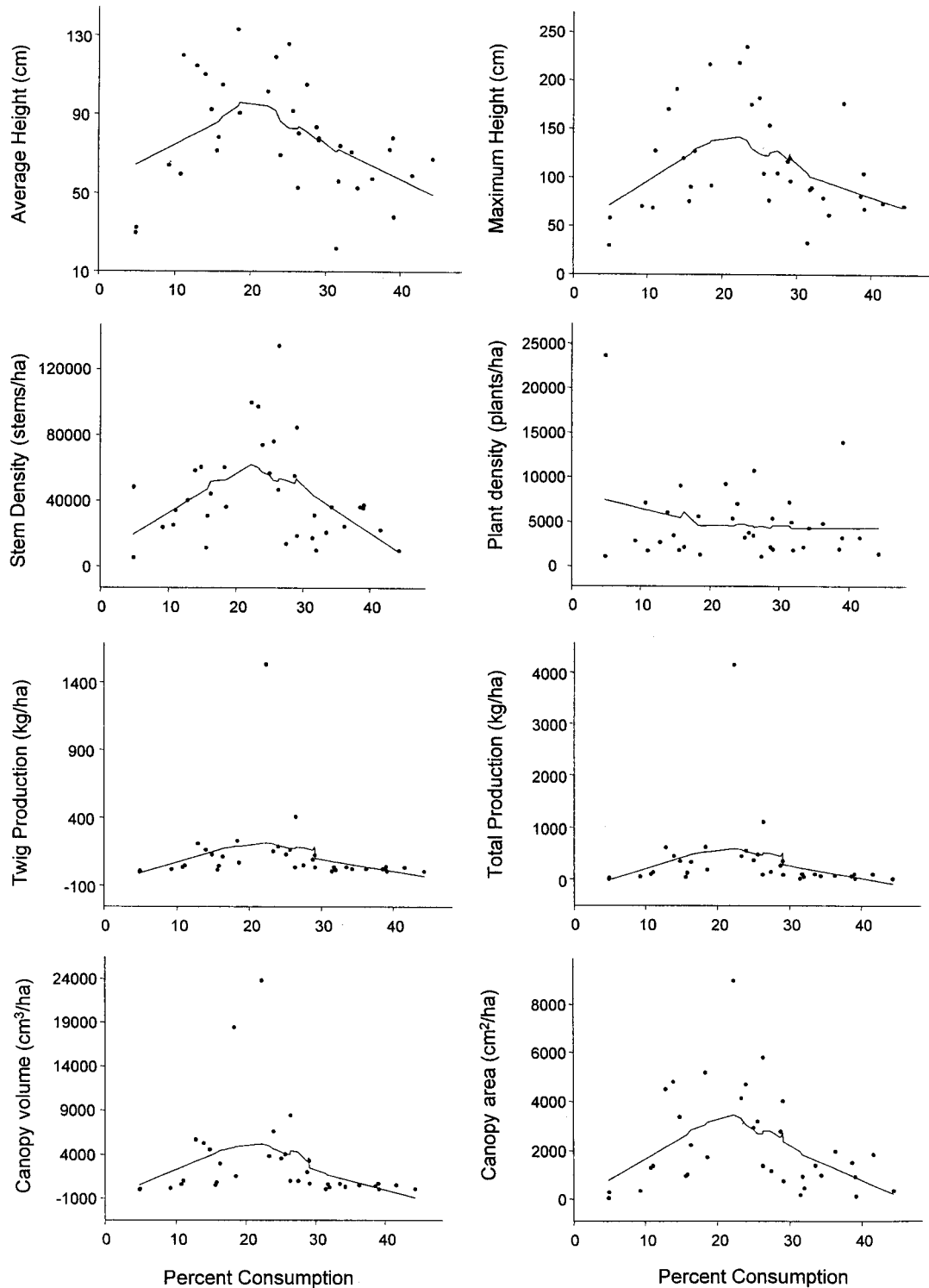
Table 2. Concluded.

Dependent variables	Elk density, 1994–1999 vs. landscape sites sampled in 1996 (n = 31)	Elk density alone 1994–1999 (n = 35)	Elk density and depth to the water table (n = 35)	Elk consumption, consumption <sup>2</sup> (n = 35)	Elk consumption, consumption <sup>2</sup> , and depth to the water table (n = 35)
Willow plant density/plot					
$r^2 =$	0.101	0.037	0.039	0.009	0.049
F =	3.28	0.40	0.30	0.14	0.54
P =	0.081	0.753	0.87	0.87	0.66
AIC <sub>c</sub> =	0.94	0.54	0.61	0.62	0.67
d.f. =	30	34	34	34	34
Twig production					
$r^2 =$	0.11	0.406	0.455	0.467	0.468
F =	3.67	7.08	6.27	14.01	9.10
P =	0.06	0.0009	0.0009	0.0001	0.002
AIC <sub>c</sub> =	1.94	1.30	1.26	1.27	1.34
d.f. =	30	34	34	34	34
Willow canopy volume/plot					
$r^2 =$	0.083	0.427	0.483	0.51	0.51
F =	2.62	7.71	7.00	16.69	10.79
P =	0.117	0.0005	0.0004	0.37	0.0001
AIC <sub>c</sub> =	2.01	1.70	1.67	1.61	1.69
d.f. =	30	34	34	34	34
Willow canopy area/plot					
$r^2 =$	0.07	0.304	0.337	0.386	0.387
F =	2.23	4.51	4.54	10.06	6.51
P =	0.146	0.010	0.0004	0.0004	0.002
AIC <sub>c</sub> =	1.17	1.12	1.07	1.06	1.14
d.f. =	30	34	34	34	34





**Fig. 6.** Elk density (elk/km<sup>2</sup>) compared to eight willow growth parameters for Rocky Mountain National Park, Colorado 1995, 1996, and 1998.



**Fig. 7.** Elk consumption rate (% offtake) compared to eight willow growth parameters for Rocky Mountain National Park, Colorado 1995, 1996, and 1998.

Table 3). No significant differences in plant diversity indices were evident in upland bitterbrush sites (Table 3). No differences in productivity of native or exotic species were observed between grazed willow and upland sites and sites that were ungrazed for 4 years ( $P > 0.20$ ).

### *Any Evidence for Potential Overgrazing*

A number of alterations to plant cover, soil, and plant abundance were observed that might meet the stated criteria for overgrazing. For example, willow production, willow height, and willow catkin production were lower on grazed sites compared to sites ungrazed for 4 years (Fig. 8). These willow responses were even more dramatic following 35 years of exclosure protection. There was more willow canopy area ( $P = 0.07$ ), more willow canopy volume ( $P = 0.08$ ), 265% higher stem density of willows ( $P = 0.19$ ), and 244% taller willow heights ( $P = 0.10$ ) in ungrazed plots. Shrub volume and shrub canopy area were also greater ( $P < 0.001$ ) in ungrazed plots following 35 years of protection for big sagebrush, *A. tridentata*, (300% and 178% higher, respectively). These changes were accompanied by increases in *P. tridentata*, *Chrysothamnus viscidiflorus*, and *Ribes* spp. on the grazed plots (824% more total shrub volume and 665% more shrub canopy cover for these three species pooled). There were also some minor changes in the soil surface due to elk herbivory that would promote erosion. Soil bulk densities were slightly (1.7%) higher on grazed sites, there was 4.6% more bare ground on grazed sites following 4 years of protection ( $P = 0.03$ ), and 6.4% more following 35 years, although this latter difference only approached statistical significance ( $P = 0.14$ ).

A number of other samplings provided little evidence for any of the stated criteria for overgrazing. There were very minor alterations to macronutrients in plants, and no general trend towards depletion of macronutrients as predicted under overgrazing (aboveground N availability is presented in Schoenecker et al., this volume). The only differences noted in macronutrients in 171 plants sampled were increases in calcium and potassium on grazed sites for one willow species (*S. monticola*), but lower phosphorous for some willows on grazed sites (Table 4). There were very few, and almost no consistent, differences in the abundance of herbaceous species following 4 years of protection. Biomass of *Solidago* spp. was more abundant on grazed sites, while *Mertensia ciliata* was less abundant. Two

species were altered more dramatically following 4 years of protection. Live cover of *Artemisia ludoviciana* was 62% less, cover of *Eriogonum umbellatum* was 50% less, and cover of accumulated herbaceous litter was 56% less on grazed sites. We found no differences in biomass of fine (mostly herbaceous) roots or N concentration in roots following 4 years of protection. But there was 850% greater biomass of coarse roots (still mostly herbaceous roots) in grazed upland sites compared to sites protected for 4 years ( $P = 0.02$ ), and there was 364% more biomass of coarse roots in grazed willow sites compared to sites protected for 35 years ( $P = 0.03$ ). After 35 years of treatment in willow type, we found differences in fine root biomass ( $P < 0.001$ ), fine root N concentration ( $P = 0.003$ ) and N yield ( $P = 0.10$ ), but not in upland grass/shrub communities.

### *Elk Consumption Rates*

Consumption of willow species averaged  $27 \pm 2\%$  in winter (Table 5). Willow consumption was greater in short willow ( $34 \pm 4\%$ ) than tall willow sites ( $26 \pm 3\%$ ,  $P = 0.04$ ) and in Moraine Park ( $31 \pm 3\%$ ) than Horse-shoe Park ( $22 \pm 2\%$ ,  $P = 0.01$ ). Shrub consumption in willow communities was lower in summer, when it averaged  $6 \pm 0.4\%$  (Table 5).

Leader use (percent of all leaders browsed) of upland shrubs averaged  $39 \pm 5\%$  and was lower than in willow sites ( $P \leq 0.08$ ). Percent annual consumption of the CAG of upland shrubs was consistent between years ( $P \geq 0.17$ ), averaging  $12 \pm 2\%$  (range 8%–16%). Percent consumption of upland shrub CAG in summer was minimal,  $< 1\%$ .

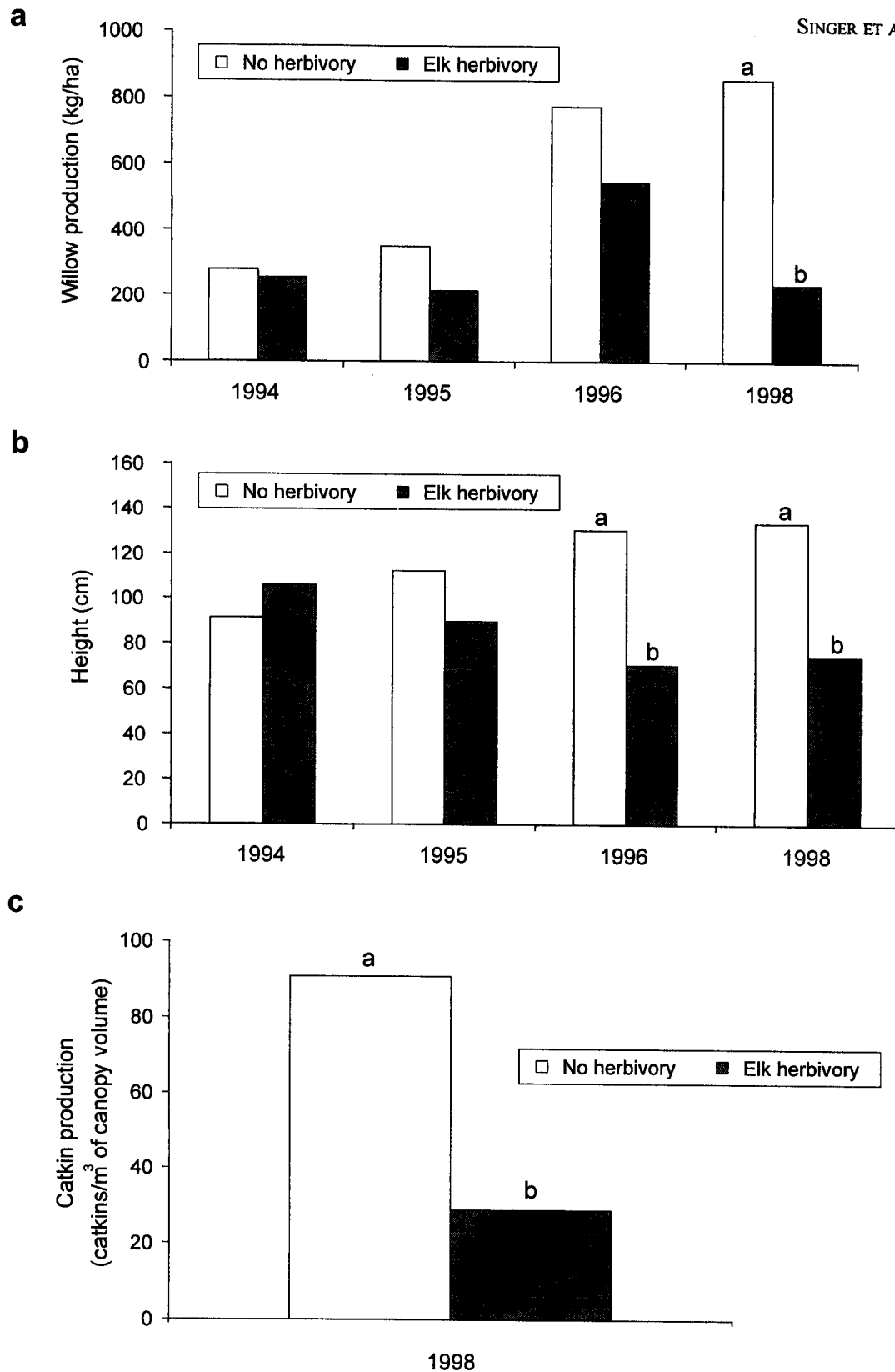
Percent consumption of herbaceous vegetation during winter was higher ( $53 \pm 9\%$ ) in bitterbrush sites than in willow sites ( $28 \pm 1\%$ ). Percent consumption of herbaceous biomass during summer averaged  $6 \pm 0.6\%$  in bitterbrush sites and  $28 \pm 9\%$  in willows. Average annual herbaceous consumption was 60% for upland bitterbrush communities and 55% for willow communities over the 4-year study period.

Overall percent consumption of herbaceous biomass in town in winter was  $30 \pm 8\%$  and did not differ ( $P = 0.91$ ) between vegetation/habitat types. Summer herbaceous consumption averaged  $29 \pm 7\%$  and did not differ greatly between types with the exception that consumption was lower ( $P = 0.06$ ) in pine-grasslands. Total annual herbaceous consumption on the study plots in town averaged 57%.

**Table 3.** Annual values for diversity indices of sampled vegetation type on elk winter range of Rocky Mountain National Park, Colorado.

Vegetation type	Year	Diversity (H)				Richness (R)			
		Grazed		Ungrazed		Grazed		Ungrazed	
		Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.
Short willow	1994	1.33	0.93–1.74	1.49	1.07–1.92	3.59	2.50–4.68	3.70	1.78–5.62
	1995	1.38	0.42–2.35	1.66	1.14–2.19	1.08	1.07–7.10	5.87	4.15–7.60
	1996	1.32	0.61–2.03	1.41	0.63–2.20	5.50	3.45–7.55	6.33	4.08–8.58
	1998	1.31	0.45–2.17	1.48	0.89–2.06	8.12	3.04–13.21	8.88	6.50–11.25
Tall willow	1994	1.02	0.45–1.59	0.83	0.06–1.61	2.91	0.44–5.38	2.30	0.13–4.47
	1995	0.92	-0.02–1.87	1.15	0.22–2.07	4.33	0.79–7.88	4.79	0.60–8.99
	1996	1.26	0.48–2.04	1.25	0.36–2.15	4.75	2.24–7.26	5.33	0.83–9.83
	1998	1.17	0.69–1.64	1.00	0.12–1.88	6.50	1.86–11.14	6.25	0.72–11.78
Upland bitterbrush	1994	1.39	0.89–1.88	1.24	0.75–1.72	3.36	2.39–4.33	2.95	1.72–4.18
	1995	1.64	0.51–2.78	1.71	1.03–2.40	4.17	1.81–6.52	3.17	1.76–4.57
	1996	1.48	0.81–2.16	1.46	1.05–1.87	5.17	3.58–6.76	4.25	3.07–5.43
	1997	1.57	1.05–2.08	1.59	1.28–1.90	5.21	4.48–5.94	5.08	3.99–6.18

c.i. = confidence interval.



**Fig. 8.** Willow production (a); heights (b); and catkin production (c) for elk grazed vs. ungrazed sites (different letters denote significant difference,  $P < 0.02$ ) on the elk winter range of Rocky Mountain National Park, Colorado.

**Table 4.** Nutrient content of willows and herbs under different herbivory treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Graminoids		Forbs		<i>Salix geyeriana</i>		<i>Salix monticola</i>		<i>Salix planifolia</i>	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Nitrogen (%)	1.74	2.00	2.48	2.51	1.14	1.08	1.18 <sup>a</sup>	1.08	1.25	1.10
Dry matter digestibility (%)	54.72	57.16 <sup>a</sup>	75.00	74.81	37.20	36.06	36.26	35.0	34.60	32.40 <sup>a</sup>
Calcium (mg/L)					0.61	0.65	0.71	0.81 <sup>a</sup>	0.62	0.65
Potassium (mg/L)					0.23	0.25	0.22	0.27 <sup>a</sup>	0.28	0.30
Phosphorus (mg/L)					0.13	0.13	0.13	0.12	0.14 <sup>a</sup>	0.13

<sup>a</sup> $P \leq 0.10$ .

**Table 5.** Percent current annual growth of shrubs consumed by elk in willow communities in Rocky Mountain National Park, Colorado.

	1994 <sup>a</sup>		1995		1996		1997		1998	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
<b>Willow</b>										
% of total leaders which have been browsed (A)	62.91	N/A	64.45	25.44	57.48	32.51			48.60	23.48
Average % of leader removed from browsed shoots (B)	58.43	N/A	32.13	35.56	46.52	19.33			32.98	28.25
% current annual growth removed (A*B)	37.14	N/A	21.61	5.76	28.08	6.91			17.09	6.93
<b>Upland bitterbrush</b>										
% of total leaders which have been browsed (A)			39.0	2.76	29.3	1.0	47.6	<1.0	33.2	
Average % of leader removed from browsed shoots (B)			25.8	N/A	28.6	28.6	33.8	9.5	31.4	
% current annual growth removed (A*B)			10.1	N/A	8.4	<1.0	16.1	<1.0	11.4	

<sup>a</sup>Winter values may be higher than other years due to variation in sampling methods.

## *Effects of Elk on Ecosystem Sustainability*

Concentrations of N in live plant tissues were not greatly altered by elk herbivory. We found increased N concentrations in only 4 of 13 grazed plants (*A. tridentata*,  $P = 0.10$ ; *Bouteloua gracilis*,  $P = 0.01$ ; *Heracleum sphondylium*,  $P = 0.09$ ; *Koeleria macrantha*,  $P = 0.01$ ). N yield (N produced/m<sup>2</sup>/year) was reduced in willow 64% following 4 years of protection ( $P = 0.05$ ). N inputs from litterfall were also reduced from 0.57 g/m<sup>2</sup>/year to 0.24 g/m<sup>2</sup>/year ( $P < 0.05$ ), although elk fecal and urinary inputs compensated for some of these losses in N inputs.

N mineralization rates were lower in grazed versus ungrazed plots of short willow sites after 4 years of protection (0.39 grazed versus 1.83 ungrazed,  $P = 0.07$ ,  $n = 4$  sites, versus 3.25 grazed and 2.11 ungrazed,  $P > 0.10$ ,  $n = 4$ , in tall willow sites; Schoenecker et al., this volume). Nitrate pools were also lower in grazed than ungrazed plots of short willow sites (0.31 grazed versus 1.44 ungrazed,  $P = 0.10$ ), but no differences for these N variables were detected in tall willows (Schoenecker et al., this volume).

From the same study plots, Schoenecker et al. (this volume) calculated that annual N inputs to the soil surface on grazed sites were only 60% (5.79g N/m<sup>2</sup>/year) from a combination of herbaceous biomass left after grazing + shrub leaf litterfall + elk urine and feces compared to ungrazed sites (9.66g N/m<sup>2</sup>/year; herbaceous biomass + litterfall). Similarly, annual N inputs to the aspen type on grazed sites were only 44% (1.65g N/m<sup>2</sup>/year) that of ungrazed sites (3.79g N/m<sup>2</sup>/year; Schoenecker et al., this volume).

## **Discussion**

### *Population-Based Predator Limitation Approach*

Our population-based estimates of food-limited  $K$  for elk in the park were strikingly similar to the nutritionally based, or food-limited, estimates of  $K$  made by Hobbs et al. (1982) ( $1,069 \pm 55$  versus  $991 \pm 102$  dry year or  $1,481 \pm 261$  wet year). The similarity of the approximation of current elk numbers in the park to the theoretical nutrition-based estimate and the observed equilibrium population size support the hypothesis that the park sub-population is currently limited through

density-dependent processes by food resources, rather than by any other factors such as predators or weather. The population-based estimate of potential food-limited  $K$  for winter in town of  $2,869 \pm 415$  elk was also similar to the forage-based estimate of food-limited  $K$  in town of  $3,082 \pm 103$  to  $3,391 \pm 113$  (average precipitation year), suggesting that  $K$  might be fairly well approximated in the town. However, we caution these estimates may be subject to errors, since elk in the town sector have not yet reached their  $K$  for winter and we selected an arbitrary value for average herbaceous forage use (50–55%) for our calculations. Thus, these town estimates should be viewed as provisional estimates.

Considerable published information from undisturbed systems with wolves and bears suggests that in pristine times, when natural densities of predators existed, elk in the RMNP system would likely have been limited below food-limited  $K$  most of the time by the large capable predators present at that time--grizzly bears, black bears, wolves, mountain lions (*Felis concolor*), and coyotes (Gasaway et al. 1992; Boyce 1993; Messier 1994). We concluded from the modeling of the northern Yellowstone elk population that limitation of the elk, on the order of about 15% fewer elk, has occurred since wolf restoration to the area, especially since 1997 (Singer et al. 2002). The northern Yellowstone elk population is similar in historic conditions to what the RMNP ecosystem must have represented. Elk are the dominant ungulate in both ecosystems, and their major predators were the same in both systems--gray wolves, grizzly bears, black bears, and coyotes. There is little additional empirical basis upon which to predict if the ultimate level of limitation of the northern Yellowstone elk population will be higher, or how consistent the limitation will be through the years, although computer models have predicted 25% or even higher levels of limitation of elk (Boyce 1993), particularly if harvests of antlerless elk by humans north of the park are not reduced (Singer and Mack 1999). Predators can act to hold ungulates at low densities for long periods (Gasaway et al. 1992; Messier 1995), especially in concert with periodic severe winters (McLaren and Peterson 1994; Mech et al. 1998). Wolf predation may act to increase the decline phase of ungulates following a peak density (since ungulates in poor condition are more vulnerable). But long-term stability under predator limitation should not always be expected by park managers. For example, predator-ungulate systems may shift between multiple equilibria (Messier 1994) due to predator-sensitive limitation and



periodic weather fluctuations (McLaren and Peterson 1994; Mech et al. 1998).

We concluded that rich forage resources in human-disturbed grass types in the Estes Valley presently compensate for the negative effects of humans on habitat and forage losses due to developments. Preliminary estimates suggest that the town sector supports only about 169 (5%) fewer elk due to these human modifications, after subtracting all the losses (the area of Estes Lake impoundment and urban areas) and adding the increases (golf courses, irrigated grasslands) to the forage biomass for elk. Nitrogen concentrations, biomass production, and N yield were higher in these human-modified grass types in town (golf courses, irrigated pastures) compared to unmodified native grasslands. Those elk that selectively feed on these human-enriched sites (e.g., elk regularly forage on the golf course) should exhibit increased foraging efficiency, increased daily energy balance, decreased winter weight losses, and improved survival (Robbins 1983; Wickstrom et al. 1984; Iason et al. 1986).

Other factors also contribute to the attractiveness of the town to elk. The developments and human activity undoubtedly contribute to less predator activity. The town is lower in elevation than park winter range and snow depths are lower. There is no sport hunting within the Estes Park town limits whereas there is limited hunting on U.S. Forest Service and private land on the edge of town. The artificially maintained forage resources in town due to annual fertilization and irrigation contribute to unnatural stability in elk numbers, since these human-managed grasslands tend to dampen natural forage fluctuations due to drought and fire. Additionally, elk using the area will be less influenced by severe winters or predators (McLaren and Peterson 1994; Mech et al. 1998; Singer et al. 1998a). Large, stochastic fluctuations in ungulate numbers are a natural process that may permit events, such as episodic recruitment in some plant groups, and these fluctuations will be less in the altered town environment. The increased number of elk in town contribute to higher overall consumption rates on the park winter ranges since town elk migrate slowly through the park winter ranges and consume vegetation during their migrations. Most radiocollared elk that wintered in town spent an additional  $64 \pm 7$  days on park winter range annually during their migration to the park's higher alpine summer range. Elk also demonstrated a high degree of habituation and willingness to graze rich forages in lawns, golf courses, and ornamental shrubs. There are almost no fences in town that obstruct elk. We predict that, in the absence of any human controls, elk

populations will continue to increase up to 47% (921 more elk over the 2001 population estimate, assuming a 50–55% use of forage) to food-limited  $K$  in the town sector, and that these additional elk will further influence the park's winter ranges during their annual migrations to the park's summer range. However, in the long-term, the  $K$  for elk in town is predicted to eventually decline as human developments continue at a rapid pace in the area.

### *Effects of Elk on Plant Community and Plant Species Diversity*

No indications of any large species shifts or declines in herbaceous plant species diversity due to elk herbivory after 4 years of protection from elk were found. These observations were in agreement with the independent findings of Stohlgren et al. (1999) for the same area. The abundance of only four herbaceous plant species was altered by elk herbivory. But we concluded that high densities of elk contributed to a large decline in willow size, structure, and growth at both the 4-year and 35-year exclosures. High levels of elk herbivory (above a threshold of 37% consumption of willow CAG) suppressed the maximal willow height, densities, volume, and CAG, although there was compelling evidence for grazing optimization at lower levels of about 21% use of willow CAG. These suppressing effects of high elk herbivory on willow growth likely have already resulted in declines in the recruitment and abundance of willow communities and further declines are also likely. Using aerial photos, GIS, and groundtruthing, Peinetti et al. (this volume) found that tall willows declined 22% in Moraine Park and 19% in Horseshoe Park from 1946–1996.

Our data suggested elk had a much larger effect than did depth to the water table on willow growth and abundance, at least under the limited range of depths of water tables and relatively high water tables in our study (average water tables varied from 0–1 m from ground surface at our sample sites and no water table ever fell below 1 m even during July or August). Thus, willows likely root to the water table at all study sites. We studied few of the most watered sites (i.e., we did not study beaver ponds) and also no dry willow sites with deep water tables (e.g., no sites of 2 m or lower were sampled). Also, depth to water table and elk density were positively correlated at some of the study sites, i.e. the highest elk densities were found at some sites that also had very high water tables, and elk effects overwhelmed any

potential positive effects of high water at these sites. But we caution against concluding that depth to the water table was of little importance. For example, long-term climate change over the past 90 years to a warmer and drier climate may have contributed to a willow decline (although more recent conditions since 1995 have been wet and cool, Singer et al. [1998b]; Stohlgren et al. [1998]). It is not known, however, if this minor climate trend could have influenced depth to water tables. Greater precipitation and higher winter snow packs resulted in higher early growing season stream flows and higher measured water tables on the study sites (Zeigenfuss et al., this volume). Beaver declined 80%–90% on the elk winter range in the park from the 1940s through the mid-1990s (Zeigenfuss et al., this volume). As a result, stream channels are currently straighter and less complex in the lower reaches of the park's streams. There are presently fewer side channels, fewer oxbows, and fewer braided channels than was the case in 1946 aerial photos. Willow cover decreased ~20% over this same time period (Peinetti et al., this volume). Thus, this large beaver decline dewatered many areas, likely increased depth to water table at many sites, and likely contributed to the willow declines. The sites of greatest alteration and simplification of the stream channels (apparently due to the decline in beaver and the effects of their dams) corresponded tightly with the locales where willows also declined the most (Peinetti et al., this volume). We suggest the return of beaver to the entire winter range would improve growth conditions for willows and would assist willows in sustaining elk herbivory.

### *The Sustainability Approach Applied to Rocky Mountain National Park*

Elk herbivory dramatically reduced sizes of four shrub species (3 willows and 1 upland shrub), and there was a 22% decrease in herbaceous production in willow communities. However, there was no measurable effect of elk herbivory on herbaceous production in any other vegetation community. Thus, we concluded the current level of elk herbivory was sustainable for 3 shrubs, but not a fourth shrub species, and most herbaceous vegetation in two vegetation types, but not sustainable for the willows and the herbaceous production in the willow type.

A key criterion to apply the sustainability approach is whether or not soil fertility, especially N and C abundances, are sustained under the level of ungulate grazing and actions of ungulates. We concluded that N

and C abundances were apparently being maintained in the upland grass/shrub type, but that N processes and N pools were being reduced by elk grazing in the willow and aspen types. Annual inputs of N under elk herbivory were only about 60% in the willow type and about 44% in aspen type compared to ungrazed sites, and N mineralization rates were 79% lower in grazed willow sites (Schoenecker et al., this volume). Most authors report an increase in N cycling rates (Risser and Parton 1982) and increased N mineralization (Ruess and McNaughton 1987; Frank and Groffman 1998) with grazing by native ungulates due to the transfer of litter to more usable fecal and urinary inputs. But several other authors have also reported a decline in N mineralization and N availability due to ungulate herbivory (McInnes et al. 1992; Ritchie et al. 1998), attributed in some cases to heavy grazing levels (Seagle et al. 1992; Biondini et al. 1998). Although feedbacks to the elk population may eventually slow or stabilize the declines in soil fertility, we caution managers that at some point, the depletions might result in declines in plant growth and changes in species composition (McInnes et al. 1992; Ritchie et al. 1998).

We found an increase in N concentrations in only one-third of the plant species we sampled. A number of studies documented higher N concentrations in grazed plants, especially grasses, apparently due to higher N uptake rate by roots of grazed plants, and greater availability of N to plants due to higher net N mineralization on grazed sites (Coughenour et al. 1990; Holland and Detling 1990; Singer and Harter 1996; Frank and Groffman 1998).

Nitrate ( $\text{NO}_3^-$ ) pools were 78% lower in grazed short willow sites in RMNP (Schoenecker et al., this volume). Variable results have been reported for effects of native ungulate grazing on N and C pools. Some authors reported no overall effect of ungulates on soil N and C pools (Frank and Groffman 1998; Ritchie et al. 1998), or even a decrease in these pools (McInnes et al. 1992; Pastor et al. 1993).

Convincing evidence for browsing optimization in willows at moderate consumption rates was found (higher willow production occurred at 21% consumption of CAG than with no consumption). Danell et al. (1985) and Oldemeyer (1981) also reported browsing optimization at moderate consumption rates for birches (*Betula* spp.). But we found no evidence for grazing optimization in herbaceous plants, in agreement with Biondini et al. (1998) and Mazancourt et al. (1998) who found no optimization, although others found evidence

for herbaceous grazing optimization by ungulates in Africa (McNaughton 1979, 1983, 1993) and in the western U.S. (Frank and McNaughton 1993).

Aboveground production might be (temporarily) maintained at the expense of belowground biomass (Belsky 1986; Verkaar 1992), and thus any assessment of grazing sustainability should include root responses (Verkaar 1992). We concluded that grazing generally resulted in no reduction of root biomass. The majority of studies report a decline in root biomass due to ungulate herbivory (Detling 1988; Coughenour et al. 1990; Holland and Detling 1990), but in support of our findings, a recent study of 11 locations in the Serengeti, Africa (McNaughton et al. 1998) found no evidence for decreases in root biomass even under intense herbivory by large numbers of wild ungulates, nor did Coughenour (1991) or Merrill et al. (1993) find any effect of ungulates on herbaceous root biomass in YNP.

### *Evidence for Overgrazing*

A key criterion of the overgrazing approach is that excess grazing leads to more bare ground and accelerated sediment yields and erosion (Pengelly 1963; Westoby et al. 1989; Fuls 1992). Elk grazing in RMNP slightly increased upper soil bulk densities (1.7%) and slightly increased the percent of bare ground (4.6%). Accelerated sediment yield is a product of not only bulk density and bare ground, but also percent plant cover, infiltration rates, and slope. For the steep slopes of an elk winter range along the Gallatin River, Montana, Packer (1963) recommended that soil surface bulk densities be below 1.04 g/cm<sup>3</sup> and percent bare ground be less than 30% to protect soil surfaces from accelerated erosion. If Packer's (1963) data can be generalized, sediment yield should not be a concern on most of the RMNP winter range since the area consists of mostly flat sites and very gentle slopes. But the percent bare ground on wet meadow and upland grass/shrub ( $\bar{x}$  = 28% wet meadows,  $\bar{x}$  = 38% upland grass) approached or exceeded Packer's (1963) thresholds of concern as did observed bulk densities on grazed sites in three vegetation types (0.81 g/cm<sup>3</sup> in meadow, 0.92 g/cm<sup>3</sup> in aspen, 1.10 g/cm<sup>3</sup> in upland grass/shrub). These values suggest there might be some concern for accelerated erosion on steeper slopes on the winter range in the upland grass/shrub type, but specific research into measures of sediment yield would be required.

Another stated criterion of overgrazing is that shifts in plant species composition will occur, and in particular, less palatable forage species will increase (Pengelly 1963;

Westoby et al. 1989; Fuls 1992). We observed little evidence for any significant increase in less palatable plant species due to elk herbivory in the willow or upland types. Stohlgren et al. (1999) also found no consistent effect of elk herbivory on plant diversity at the landscape scale in these same types. Several less palatable species (*Phleum pratense*, *Carex* spp., *Selaginella densa*) increased during 25 years on open range plots (grazed sites only with no controls) in the upland grass and meadow types on the winter range (Zeigenfuss et al. 1999). We interpret the increases in herbaceous root biomass in the grazed willow and upland type as an underground response to the declines in shrubs (*Salix* spp. and *Artemisia tridentata*) due to grazing. We did not excavate or sample shrub root systems, but we suspect these declined on the grazed sites.

### *The Allowable Use Approach Applied to National Parks*

No magic golden rule exists in the literature for allowable use that could be unambiguously applied to a number of national parks. In contrast to any general rules, the published literature we reviewed suggests plant response to ungulate herbivory varied greatly between different ecoareas (Coughenour 1985; Milchunas et al. 1988; see review in Fig. 2). Our review indicated that, in general, plants growing in sites with higher N and water availability seemingly tolerated higher rates of herbivory (Hamilton et al. 1998; Mazancourt et al. 1998) and plants with a larger proportion of their biomass in roots, such as occurs in the shortgrass prairie and some other grasslands, also tolerated herbivory better. The timing of the herbivory also influenced plant responses (Mueggler 1975; Frank and McNaughton 1992) with fewer effects predicted from winter herbivory than from herbivory during the growing season. Herbivory during winter only is better sustained since the plants are in senescence, the ground is frozen, and the plants' reserves are shunted to the root systems and the ground is frozen and/or protected by snow cover to some extent from hoof action of ungulates (Frank and McNaughton 1992; Singer and Harter 1996; Singer et al. 1998b).

Consumption rates in those grassland types most similar to RMNP (e.g., mountain bunchgrass, mixed grass prairie; Fig. 2) that evolved with at least moderate herds of grazing ungulates (40–45%) appeared to be sustainable in most instances, but consumption rates of 60–80% were not. Exceptions were the more grazing resilient short grass prairie and the Serengeti grasslands, where higher consumption rates of 60–65% by ungulates

were apparently sustainable. The RMNP grasslands will not be quite as resilient as the short grass prairie or the Serengeti grasslands, since both of those areas adapted to, and evolved with, grazing by large herds of ungulates (e.g., Serengeti: African buffalo, wildebeest, zebra; short-grass prairie: American bison). The current high consumption rate of 60% (averaged over 4 years) in upland grass/bitterbrush type, in the RMNP case example might be a concern to management based on the published literature. These high consumption rates have probably been limited to the previous 8–12 years. We suspect that, if maintained, these high consumptions could possibly result in future vegetation changes in the park, especially if elk in the town sector are allowed to further increase to their estimated potential and if consumption rates of plants in the park increase due to more town elk migrating through the park's winter range.

Our review indicated that, in general, productive, seral shrub communities (i.e., willow, aspen, birch, mountain maple) could typically sustain consumption rates of 42–50%, but consumption rates of 65–85% are not sustainable (Fig. 2). These published findings, many that are based on artificial clipping studies, predict the range of willow consumption rates we observed in RMNP should have no negative influences on willows (Aldous 1952; Krefting et al. 1966; Wolff and Zasada 1979; Wolfe et al. 1983; Bergström and Danell 1987). Yet, we observed substantial reductions in willow heights, volumes, and production at 37% consumption rates by elk. This discrepancy is apparently due to the fact that much of the information on shrubs is based on clipping studies to simulate herbivory. These studies assume artificial clipping mimics ungulate herbivory, but we conclude it does not. The effects of ungulate herbivory on willows in this study were roughly two-and-a-half times greater than equivalent CAG removal by clipping (Zeigenfuss et al., this volume). The physical damage from elk (rough breakage, stripping of bark) has a greater effect on willows than the clean, mechanical clipping of shoots. For example, an average of 20% of the adjacent length of a browsed leader died after winter browsing by elk in our study area, but only 2% of the leader died after mechanical clipping (Menezes et al. 2001).

Our review suggests upland shrubs of the Intermountain West generally sustained ungulate consumption rates of 24–28% CAG, while higher studied consumption rates of 55–68% were not sustainable. In the case example of RMNP, we found big sagebrush was more sensitive to removals than suggested by the literature. Although we

found no effect on any upland shrubs due to grazing by elk at levels of 12% consumption of CAG following 4 years of protection, we found large size reduction in grazed sagebrush following longer periods (35 years) of grazing compared to ungrazed plants. However, three other upland shrub species actually increased slightly on these same grazed areas compared to ungrazed areas following 35 years of protection.

## Conclusions

### *The Overgrazing Approach*

The criteria for overgrazing are the most clearly stated and most simply and readily measured of any of the approaches, and thus we recommend this view be applied as the first choice in clear cut cases where, clearly, there is either overgrazing (i.e., many of the criteria for overgrazing can be documented), or in those cases where there is no evidence of overgrazing (i.e., when none or almost none of the criteria for overgrazing can be documented).

Unfortunately, most cases will fall into an intermediate category of observed criteria for overgrazing, as did the RMNP case example. Here we found the overgrazing approach to be less than adequate. Considerable judgments as to the severity of evidence will be required in these instances. In the RMNP data set, we investigated 20 enclosure comparisons that might constitute evidence of overgrazing, and only four of these comparisons met the criteria for overgrazing (less big sagebrush production, less willow production, less herbaceous production, more bare ground). For a fifth criteria, that of possible accelerated erosion, our measures indicated a concern in only one vegetation type. Does this mix of evidence for RMNP data constitute evidence for overgrazing or not? Another concern over this approach is that it was developed for agricultural systems. But, natural ungulate grazing might result in some increase in bare ground and some effects on plants, and many of their other actions (dusting, rubbing trees and shrubs, hoof action on soil compaction) must be viewed as natural effects. The variables measured for overgrazing criteria (e.g., percent bare ground, sediment yield, percent plant cover, trampling) may represent a very simplistic view of ecosystem dynamics and plant-herbivore relations as Westoby et al. (1989), Coughenour and Singer (1991), and McNaughton (1993) have pointed out.

### *The Allowable Use Approach*

We recommend the application of allowable use criteria to national parks as another highly useful approach to managers, but only in cases where considerable empirical data are available for that area on effects of different levels of use. The principal disadvantages of this approach for widespread use are that, as our literature review suggested, there are few general rules that could be readily applied to a new study area with little background data (see Fig. 2). The response of plants to a specific use level will vary depending on the ecosystem type, the structure and growth form of the plants, and the extent of evolution with ungulate grazing (Fig. 2; McNaughton 1979, 1983; Milchunas et al. 1988). In the case example, of RMNP, a large amount of ecological information gathered by us and other researchers is available to apply the allowable use approach.

The advantage of this approach is that it provides a straightforward, quantitative measure of the direct interaction between herbivores and their plant forages, providing that specific information is available for the park. The approach provides the opportunity to set very specific vegetation goals. For example, should NPS managers decide, based on historical conditions and natural processes, that the current decline in willows in RMNP is a departure from natural conditions, the allowable use information we gathered suggest the current average rate of consumption of willows in the park winter range should be lowered from 27% to less than 21% (an approximate 22% decrease in average use). This would apparently protect most willow patches from overuse. This goal might be achieved by reducing the elk population in the park by roughly 22% to 838 elk, ( $1,074 \text{ elk} \times 0.78$ ). This reduction is also roughly similar to the reduction (20–30%) suggested by the predator limitation estimates for YNP (Singer et al. 2002). We do caution, however, that this assumes a linear reduction in willow consumption and that elk distributions remain constant, neither of which might hold true. Management decisions still must be made as to the natural conditions and processes that prevailed in the park area and, thus, what effects of a specific use level by ungulates on plants will be acceptable and what effects are excessive.

### *The Biodiversity and Sustainability Approaches*

We concluded that both the diversity and grazing optimization/sustainability approaches would be

ambiguous and complex for most park managers to apply to a new assignment to an ecosystem question, although the approaches could be useful in well-studied and well-understood ecosystems. In human-altered systems, it is challenging to determine what influences of ungulates might be natural and acceptable. For example, ungulates in pristine, natural systems may alternatively increase, cause no change, or decrease plant diversity (McNaughton 1979, 1993; Stohlgren et al. 1999) or plant production (McNaughton 1983, 1993; Frank and McNaughton 1993; Biondini et al. 1998). Which response is the most appropriate in the particular natural system under observation? There may be no one single answer. Application of these approaches requires an understanding of the complex ecological relationships of that ecosystem. A sound scientific appreciation for which observed plant changes are due to factors other than ungulates (such as succession, climate change, fire suppression, or beaver declines) needs to be isolated from changes in the system that are due to ungulates alone. Use of these two approaches should not be ruled out by managers to evaluate ungulate effects, but a commitment of many years and much effort will likely be required to understand the ecosystem dynamics sufficiently to apply the views.

These two approaches, however, could be readily applied to a park such as the RMNP case example where there is extensive information on plant species and vegetation community diversity responses to ecosystem processes, such as succession, herbivory, fire, and fluvial processes (Olmstead 1979; Stohlgren et al. 1999; Zeigenfuss et al., this volume). One advantage of applying these approaches is that both are closely aligned to the NPS mandates to manage for diversity and maintain natural ecosystem processes (NPS 2001).

### *The Population-Based Predator Limitation Approaches*

As our first choice for the most useful and most general approach for use by NPS managers, we selected the population-based or forage-based estimates of food-limited  $K$  applied in concert with actual observations of the extent of predator limitation of ungulates below food-limited  $K$  in that, or in similar, ecosystems. This approach is the most central and closely aligned to NPS policy, which calls for preservation of natural processes. One of, if not the most important natural process, includes the effects of large, capable predators on ungulates.

The population-based and forage-based estimates of food-limited  $K$  were also operationally clear, i.e., the methods were specific, quantifiable, and measurable (Table 6). Population-based estimates of  $K$  compared favorably (only ~7% different) to independent nutritionally-based estimates of  $K$ , lending credence to the accuracy of both independent estimates. Any possible management intervention would most readily be based on elk population size goals; thus, population-based analyses will be central to those goals. We concluded multiple natural predators in the RMNP ecosystem would have likely limited ungulates below density-dependent or food-limited  $K$  for elk during most years (Gasaway et al. 1992; Messier 1994; Sinclair and Pech 1996; Orians et al. 1997; Mech et al. 1998). The challenge to applying this approach is that the magnitude and duration of predator-limitation may not always be sufficiently understood and may be difficult to predict for a specific park area (Boutin 1992; Sinclair and Pech 1996; Crete 1998). Also, these approaches may require long-term data sets. For example, the detection of density dependence may require reduction of the ungulate population to less than or equal to one-fourth of  $K$  prior to any release (Shenk et al. 1998). Detection of density dependence, which is necessary to estimate food-limited  $K$  from the population growth trajectory, is often detected only after large ( $\geq 75\%$ ) reductions in animals, subsequent release of the population, and, finally, observation of the population growth trajectory for 12–18 years following release (Coughenour and Singer 1996; Shenk et al. 1998; McCullough 1999; this study in RMNP). This kind of unique information may not be available for many parks, but the information was available for our case study in RMNP.

The evidence for multiple predator limitation of elk in Yellowstone National Park, Wyoming following wolf restoration in 1995 should provide a useful starting number for the likely limitation of elk by multiple predators in a continental Rocky Mountain ecosystem. Computer modeling projected that the limitation of elk by wolves, in concert with other predators, in YNP is currently about 15% less than food- and weather-limited  $K$ , and additional limitation is possible (Singer et al. 2002). Wolves may also be altering the distributions of elk in Yellowstone National Park and their foraging patterns across the landscape (Ripple and Larsen 2000). Where there is specific information on the effects of predators, this approach requires more straight-forward interpretation of natural conditions.

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**Table 6.** Summary of the consequences for the application of five approaches for evaluating overabundance of ungulates in national parks.

	Approach to Evaluate Ungulate Abundance				
	Population-based	Biodiversity	Grazing optimization/ sustainability	Overgrazing	Allowable use
Operational clarity: Specific, quantifiable, and readily measurable	Moderate to high. Population parameters and <i>K</i> are measurable. Pristine conditions may not be known.	Low. Controls and other confounding variables may not be available.	High. ANPP and consumption readily measurable.	High. Only exclosures are needed.	Low, excessive and sustainable levels are rarely tested.
Relative time and costs	High. Large popula- tion perturbation or manipulation is necessary. 20–30 years of response may be needed.	Moderate. Sufficient time for grazing responses may require many years.	High. Sampling of nutrients and processes can be intensive and expensive.	Low to moderate. A number of years response may be needed, but measures are rapid and some evaluations will be immediately obvious.	Moderate. 4 years of plant data are required and costs for intensive plot sampling are moderate.
Elk management consequences	(a) Food-limited <i>K</i> . None to little management of the ungulate. (b) Simulate predator limitation. High. Frequent removal of animals will be necessary. Possible removals of animals or actions such as translocations or brief harassment hunts to alter distribution.	Possible reductions in elk may be necessary.	Depends on findings, can be minimal to a high level of management necessary.	Depends on findings.	Elk population is managed to obtain appropriate allowable use level.
Plant management consequences	Plant responses are predicted to follow the population goals of the ungulate.	Possible plantings, temporary exclosures or burnings to mitigate any ungulate overabundance.	Depends on findings.	Depends on findings.	Depends on findings.
Time required for a measurable feedback	Immediate.	Slow, possibly >20 years.	Rapid, a few years.	Slow.	Rapid.

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**Appendix A.** Vegetation coverage of major elk winter ranges in eastern Rocky Mountain National Park, Colorado.

Cover class	Horseshoe Range		Moraine Range		Trail Ridge Range	
	Area (km <sup>2</sup> )	Percent	Area (km <sup>2</sup> )	Percent	Area (km <sup>2</sup> )	Percent
Water	0.30	1	0.39	1	0.16	1
Willow	5.59	9	5.06	11	1.93	9
Grassland	3.57	6	4.14	10	2.55	12
Shrubland	2.57	4	2.23	5	0.80	4
Unvegetated	0.16	0	0.15	0	2.58	12
Aspen	0.23	0	0.22	1	0.03	0
Conifer	46.36	75	29.55	68	0.00	0
Pine grasslands	3.28	5	1.51	4	0.00	0
Subalpine forest	0.06	0	0.00	0	2.25	10
Tundra	0.00	0	0.00	0	0.137	1
Alpine range	0.00	0	0.00	0	11.07	51
Total	62.08	100	43.14	100	21.50	100

**Appendix B.** Vegetation coverage for the town winter elk range, Estes Park, Colorado.

Cover class	Area (km <sup>2</sup> )	Percent
Shrubland	4.87	8.0
Grassland	13.83	22.8
Aspen	0.09	<1
Ponderosa pine	22.46	37.0
Douglas fir	0.36	<1
Lodgepole pine	7.08	11.7
Unvegetated	0.72	1.2
Water	0.80	1.3
Disturbed grasslands	2.91	4.8
Slightly irrigated grasslands	2.82	4.5
Subirrigated grasslands	0.52	<1
Golf course	0.62	1.0
Willow	3.60	5.9
Total	60.68	100

**Appendix C.** Indices used to measure herbaceous species diversity in grazed and ungrazed plots on elk winter range in Rocky Mountain National Park, Colorado.

Index	Formula	Source
Diversity	$H = - \sum_{k=1}^s (P_k) \ln(P_k)$	Shannon and Weaver (1962)
Richness	$R = s/\text{total number of plots}$	

$P_k$  = the proportion of total biomass contributed by species K.

S = the number of species observed in a plot.

**Appendix D.** Primary components (>5%) of elk diets in Rocky Mountain National Park, 1994–1997.

Seasonal range	Genus	Percent of total diet by season			
		Spring	Summer	Winter	Fall
Alpine	<i>Salix</i>	6.9	57.0		
	<i>Pinus</i>	42.3			
	<i>Carex</i>	20.0	17.6		
	<i>Stipa</i>	7.6	4.3		
	<i>Pseudotsuga</i>	6.6			
	<i>Artemisia tridentata</i>		9.1		
	Other graminoids	9.4	4.2		
	Other forbs	4.8	6.0		
	Other woody browse	2.1	1.5		
Low elevation winter	<i>Salix</i>	9.7		10.2	15.2
	<i>Pinus</i>	6.0		12.6	8.1
	<i>Carex</i>	26.8		9.3	8.2
	<i>Stipa</i>	27.4		28.0	26.5
	<i>Poa</i>			8.2	8.6
	<i>Agropyron</i>			8.3	
	<i>Juncus</i>	8.6		8.7	6.9
	<i>Phleum</i>				5.3
	Other graminoids	13.8		8.1	9.7
	Other forbs	5.7		4.5	9.7
	Other woody browse	1.8		1.8	1.4